

**THE EFFECTS OF ELEPHANT AND MESOHERBIVORES  
ON WOODY VEGETATION**

by

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## **ABSTRACT**

Herbivores are important drivers and have a longstanding history in shaping our terrestrial environments. However, during the past decades, changes in woody vegetation in savanna and forest systems have been observed in southern Africa. Subsequently, concerns have been raised about the loss of (tall) trees in areas with elephant. The relative effects of browsing herbivores on vegetation and the potential browsing interaction with other herbivore species remain unclear and were examined using vegetation transects and exclosure experiments in savanna woodland and Sand Forest.

Rainfall, fire and elephant were important savanna determinants. Especially rainfall positively affected woody densities, which were negatively affected by a longer exposure time to elephant, but not to elephant densities itself. In general, within South Africa's savannas, tree height classes were absent from the population demography. Different height classes were likely to be impacted by different drivers. For example, seedling and sapling densities were greater with longer fire return periods and increased rainfall. The Sand Forest exclosure experiments showed that forest regeneration was impacted by nyala and both elephant and nyala, as the absence of both species increased tree densities. Both species combined, and individually, also affected tree species assemblages. In contrast, short term elephant access to a savanna area did not affect tree densities or species assemblages. In both savanna and Sand Forest elephant displaced mesoherbivores, and in Sand Forest both elephant and mesoherbivores displaced their smaller counterparts. The presence of competitive displacement also affected recruitment (i.e. seedlings and/or saplings) of woody vegetation both in Sand Forest and savanna.

Thus, elephant and mesoherbivores exert direct and indirect (i.e. competitive displacement providing a window for recruitment) impact on vegetation. Active management of the herbivore species assemblage affects both vegetation and other herbivores, which effects potentially cascade into lower trophic levels, jeopardising biodiversity and ecosystem processes. Therefore, the full herbivore assemblage present and their combined and individual browsing effects need to be considered when setting management goals to conserve habitats and biodiversity across all trophic levels. In addition some contrasting results between Sand Forest and savanna emphasise the need for caution when extrapolating results from different areas and ecosystems.

## **PREFACE**

The field work described in this thesis was carried out in the Phinda Private Game Reserve and Ukhozi in Balule Private Game Reserve, through the School of Biological and Conservation Sciences, University of KwaZulu-Natal, Durban, from July 2006 to May 2010, under the supervision of Professor Rob Slotow and co-supervision of Mr Bruce Page.

These studies represent original work by the author and have not otherwise been submitted in any form for any degree or diploma to any tertiary institution. Where use has been made of the work of others it is duly acknowledged in the text.

The chapters in this thesis may differ in lay-out meeting specific requirements of the journals the chapters have been published with or have been submitted to.

Georgette Lagendijk

September 30, 2011

## **DECLARATION 1 - PLAGIARISM**

I, Daisy Diana Georgette Lagendijk declare that

1. The research reported in this thesis, except where otherwise indicated, is my original research.
2. This thesis has not been submitted for any degree or examination at any other university.
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## DECLARATION 2 - PUBLICATIONS

DETAILS OF CONTRIBUTION TO PUBLICATIONS that form part and/or include research presented in this thesis (include publications in preparation, submitted, *in press* and published and give details of the contributions of each author to the experimental work and writing of each publication)

### Publication 1:

Lagendijk, D.D.G. & Slotow, R. Rainfall, elephant and fire affect height class distributions of woody vegetation in South African savannas

This paper is in preparation for submission to *Ecology*. The first and second authors are responsible for the design of the study; the first author analysed the data; the paper was written by the first author with helpful comments and revisions from the co-author.

### Publication 2:

Lagendijk, D.D.G, Thaker, M., De Boer, W.F., Page, B.R., Prins, H.H.T. & Slotow, R. Woody vegetation communities and herbivory in a South African savanna: effects of landscape position and elephant

This paper is under review with the *European Journal of Wildlife Research*. The first, fourth and sixth author are responsible for the design of the study; the first author performed the research and analysed the data; the paper was written by the first author with helpful comments and revisions from the other authors.

### Publication 3:

Lagendijk, D.D.G, Mackey, R.L., Page, B.R. & Slotow, R. (2011) The effects of herbivory by a mega- and mesoherbivore on tree recruitment in Sand Forest, South Africa. **PLoS ONE** 6(3): e17983

The first, third and fourth author are responsible for the design of the study; the first author performed the research; data was analysed by the first and second author; the paper was written by the first author with helpful comments and revisions from the other three authors.

Publication 4:

Lagendijk, D.D.G, Page, B.R. & Slotow, R. (2011) Short term effects of single species browsing release of different-sized herbivores on Sand Forest vegetation community, South Africa.

**Biotropica** DOI: 10.1111/j.1744-7429.2011.00776.x

The first, second and third author are responsible for the design of the study; the first author performed the research and analysed the data; the paper was written by the first author with helpful comments and revisions from the other two authors.

Signed:

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**LIST OF ABBREVIATIONS**

ANOVA	analysis of variance
$\beta_{co}$	Code's measure of beta-diversity
<i>B</i>	diet breadth
BIO-ENV	linking biotic to environmental patterns procedure
Ca	Calcium
Cu	Copper
$D_i$	average density for class midpoint ( $M_i$ )
ECEC	effective cation exchange capacity
GPS	global positioning system
K	Potassium
$M_i$	class midpoint
MANOVA	multivariate analysis of variance
Mg	Magnesium
Mn	Manganese
$\bar{O}$	diet overlap
P	Phosphorus
<i>PROTEST</i>	<i>PRO</i> crustean randomisation <i>TEST</i>
$R_{ca}$	relative change in abundance
<i>RP</i>	fire return period
SCD	size class distribution
Total N	Total Nitrogen
Zn	Zinc
+E+N	elephant present, nyala present
-E+N	elephant absent, nyala present
-E-N	elephant absent, nyala absent

## CHAPTER 1

### General Introduction

Conservation of terrestrial ecosystems is of crucial importance for retaining ecosystem services, such as carbon sequestration, food and fuel (Clarke & Grundy 2004; Egoh et al. 2009; Shackleton & Scholes 2011). These ecosystem services are the product of ecosystem processes, which occur through interactions between biotic and abiotic elements within the ecosystem (Diaz & Cabidoz 2001). One such process is primary production on which most of terrestrial life is dependent (Melillo et al. 1993).

Primary production takes place through vegetation, which sustains life through the provision of, amongst others, oxygen and food (Clarke & Grundy 2004). The type of vegetation and vegetation dynamics, and thus also primary production, are determined by drivers such as climate (e.g. rainfall, solar radiation), nutrients, topography, geology, and disturbance factors such as fire, man and herbivory (Scholes & Walker 1993; Bork et al. 1997; Williams-Linera & Lorea 2009; Taylor 2010). Interaction effects exist between many of these drivers, for example, between topography and fire, and between nutrients and herbivory (Archibald et al. 2009; Pretorius et al. 2011).

Rainfall is the most important climatic factor driving vegetation dynamics (Higgins et al. 2000; Sankaran et al. 2005; Gardner 2006). Vegetation growth, and thus biomass, is determined by water availability (Gaugris et al. 2008; Van Wilgen et al. 2004). In turn, the available biomass influences herbivory patterns, which drive vegetation dynamics and composition (see below) (Russell & Fowler 2004; Levick & Rogers 2008; Midgley et al. 2010). High radiation is coupled to moisture loss and thus restricts the establishment of seedlings (Castro et al. 2004). Nutrients are important in facilitating plant growth (Scholes & Walker 1993; Grellman 2002; De Graaff et al. 2006), and are related to drivers such as topography and geology (Scholes & Walker, 1993; Grant & Scholes 2006). The effects of fire interact with rainfall (Higgins et al. 2000; Van Wilgen et al. 2004). High rainfall, increases grass biomass production, which leads to an increase in fuel load and fire intensity, and may induce tree mortality (Higgins et al. 2000; Vanak et al. 2011). Humans also affect vegetation as a disturbance factor through activities such as utilisation of natural resources (e.g. fuel wood and medicinal plants) and conservation management practices (Scholes & Walker 1993; Gaugris & Van Rooyen 2008; Shackleton & Scholes 2011). However, the emphasis in this dissertation will be on herbivory, and more specifically, on browsing by large mammalian herbivores.

Herbivores are one of the key components in shaping terrestrial ecosystems (Scholes & Walker 1993; Gordon et al. 2004). Large mammalian herbivores can be grouped into three guilds, based upon their functional food types: grazers, browsers and mixed feeders (Fritz et al. 2002; Codron et al. 2007). Grazers feed on monocotyledons (e.g. grasses), while browsers feed on dicotyledons (e.g. woody plants) (Gagnon & Chew 2000; Fritz et al. 2002). Mixed feeders, or intermediate feeders, feed on both resources, showing a temporal shift from consuming grass in summer to browse in winter (Gagnon & Chew 2000; Fritz et al. 2002).

Herbivores can also be separated, based on differences in body size, into mega-, meso- and small size herbivores. Megaherbivores are species with a body mass exceeding 1000 kg (Owen-Smith 1988). Examples of browsing megaherbivores are the African elephant *Loxodonta africana* (hereafter elephant) and black rhinoceros *Diceros bicornis*. Browsing mesoherbivores, are medium-sized species between 50 and 450 kg (Fritz et al. 2002; de Garine-Wichatitsky et al. 2004), such as greater kudu *Tragelaphus strepsiceros* and impala *Aepyceros melampus*. Common duiker *Sylvicapra grimmia* and suni *Neotragus moschatus* are examples of small size herbivores with a body mass < 50 kg (Estes 1991).

Through their foraging activities, browsing herbivores instigate direct changes in vegetation dynamics, as well as indirectly, in many complex ecological processes (Danell et al. 2003). Vegetation dynamics can be affected positively or negatively by herbivores. Ingestion of fruit, and thus seeds, may provide the required scarification treatment for germination so that seedlings may be added to the population regeneration process (Lewis 1987; Miller 1995). Forest gaps created during foraging may open up germination opportunities for other forest species (Fashing et al. 2004; Lawes et al. 2004). On the other hand however, excessive feeding may lead to the local extirpation of plant species, decrease in plant growth or to the loss of reproductive trees (Gill & Beardall 2001; Bond & Archibald 2003; O'Connor et al. 2007). At the plant level, intensity of browsing also affects levels of nutrients and phenolic compounds, therefore making plants either more or less palatable for future (re)visiting browsers (de Knecht et al. 2008; Kohi et al. 2009). The exact responses of individual plants, as well as entire communities, to herbivory (e.g. herbivore species and intensity of browsing) is not yet fully understood. Plant species composition may perhaps change under different intensities of herbivory or different herbivore species assemblages. In addition, the species specific effects of different sized herbivores still require additional research to the enclosure experiments which have been (recently) conducted (e.g. Siebert & Eckhardt 2008; Riginos & Young 2007, see below).

The aforementioned herbivory effects may cascade further into the system, by which herbivory is indirectly affecting other biota on various trophic levels, ecosystem processes and ultimately ecosystem functioning (Chapin et al. 2000; Danell et al. 2003). Well-known examples of trophic cascades are readily available from carnivore ecology (Pace et al. 1999). For example, the introduction of wolves (*Canis lupus*) in Yellowstone National Park, U.S.A., caused elk (*Cervus elaphus*) to decline, which in turn released browsing pressure on aspen (*Populus tremuloides*), enhancing their population recruitment (Ripple & Beschta 2007). An example of a two-way trophic cascade, where herbivory affected lower trophic levels which then influenced a higher trophic level comes from Tembe Elephant Park In South Africa. Species assemblages of dung beetles and spiders were altered after vegetation structure changed due to elephant disturbance (Botes et al. 2006; Haddad et al. 2010).

The most controversial of all herbivores, in terms of impact on vegetation, is elephant, a megaherbivore, with cows weighing up to 2500 kg and bulls 5000 kg (Owen-Smith 1988). Elephant, being a mixed feeder, utilise a wide range of systems, from savanna woodland to swamps and forests to grasslands, illustrating their adaptability to different vegetation types (Estes 1991). While foraging 60-75 % of the day (Owen-Smith 1988), elephant are able to consume up to 170 kg of fresh weight of browse daily (Guy 1975; Legendijk et al. 2005), with a resultant impact on vegetation.

The effects of elephant on woody vegetation have been documented in many studies (e.g. Barnes 2001; Jacobs et al. 2002; Guldmond & Van Aarde 2007; Kerley et al. 2008; Shannon et al. 2008). The foraging behaviour of elephant, which includes bark removal and toppling of trees, has been linked, amongst others to tree reductions, conversion of woodland to open savanna and local extirpation of plant species (Caughley 1976; Owen-Smith 1988; O'Connor et al. 2007; Kerley et al. 2008). Therefore elephant are keystone species, or even ecosystem engineers (Jones et al. 1994; Power et al. 1996). The removal or presence of elephant from/in the system will have a large effect on the systems' biota (Power et al. 1996), and in the case of ecosystem engineers, elephant can alter the current state of the ecosystem through its foraging activities (Jones et al. 1994). While historically elephant have been under threat from hunting, poaching and displacement by humans (see review in Carruthers et al. 2008), numbers have been increasing over the last two decades (Carruthers et al. 2008), with a concomitant effect on vegetation (Van Aarde et al. 2008). The effects of elephant on vegetation dynamics are of major concern to

conservationists (Kerley et al. 2008; Kalwij et al. 2010). In addition, elephants are also charismatic species with an enormous tourism value (Carruthers et al. 2008; Kerley et al. 2003).

Managing protected areas with the full complement of (herbivore) species is challenging when one also needs to preserve the sustainability of the ecosystem. With the expansion of human impact, the resulting land available for wildlife and conservation is limited (Joppa et al. 2008). When herbivore populations reach high numbers in many protected areas, the effects of herbivores on vegetation become more pronounced (Van Aarde et al. 2008; Kerley et al. 2008), and may consequently endanger the current ecological state (Kerley et al. 2008; Kalwij et al. 2010). A full understanding of the mechanisms of how different sized herbivores, both directly and indirectly, affect vegetation and ecosystem processes is of crucial importance.

### ***Herbivory in the African context***

The highest diversity of large herbivores can be found in Africa, predominantly within the savanna biome, which is characterised by the coexistence of grass and trees and covers 40% of the continent (Scholes & Walker 1993; Du Toit & Cumming 1999; Higgins et al. 2000; Fritz & Loison 2006). The high spatial heterogeneity allows for almost 80 different-sized herbivore species to coexist within the landscape (Owen-Smith 1988; Du Toit 2003), and thus exert impact on the vegetation. African savannas still comprise the full spectrum of different-sized herbivores (e.g. small-size, meso- and megaherbivores), which is absent from savannas in South America and Australia.

Trees have an important role in ecosystem functioning and human society through the provisioning of shelter, shade and forage or natural resources (Clarke & Grundy 2004; Monadjem & Garcelon 2005; Manning et al. 2006). The potential impact of elephants on forests and woodlands may cause mortality in trees in a range of sizes. Elephants pull out seedlings of specific species such as *Sclerocarya birrea* (G. Lagendijk, pers. obs.), but are more commonly known to induce mortality on the larger trees through pushing over and ring barking of trees (Owen-Smith 1988; Kerley et al. 2008). The latter particularly poses a threat to the population dynamics of trees, as reproductive adult trees may thus disappear from the population.

Regenerating tree populations are characterised by a high abundance of seedlings, representing sufficient recruitment, and a lower abundance of tall trees (Lykke 1998; Obiri et al. 2002). The curve of such distributions shows an inverse J-shaped frequency distribution (Lykke 1998; Obiri et al. 2002). Any different shaped distribution is indicative of disturbance (Walker 1986). The

transition of individuals through different size classes is dependent on drivers such as fire, climate, human resource utilisation and herbivory (Bond et al. 2001; Lawes et al. 2004; Bork et al. 2007; Gaugris & Van Rooyen 2007; Staver et al. 2009). However, the relative effects of these drivers on the tree demography remain unclear (Midgley et al. 2010).

Small- and mesoherbivores may be more important in structuring tree populations than elephant. In Lake Manyara, Tanzania, Prins and Van der Jeugd (1993) observed an increase in bush encroachment (i.e. vegetation change from open grassland into thicket) after outbreaks of anthrax which decreased the impala population substantially, thus providing a window for seedling recruitment. Interestingly, in a 3-year experiment in Serengeti National Park, seedlings did not grow larger than 31 cm when exposed to either browsing, or browsing and fire, but increased to 49 - 78 cm when protected from both fire and herbivory by small-size and mesoherbivores (Belsky 1984). These two examples illustrate that tree populations are affected by small-size, meso- and megaherbivores. Furthermore, while elephant open up the canopy by impacting on large trees, mesoherbivores may also have an additional effect on population structures as controllers of the state induced by megaherbivores. Mesoherbivores may suppress woodland or forest recovery through browsing after megaherbivore impact has altered woodland to shrubland (Pickett et al. 2003).

The real threat to the current state of savanna woodlands and forests will therefore be when individual plant species or entire vegetation communities disappear over time. The effects of natural die-offs, fire or megaherbivores cannot be compensated when there is no adequate recruitment and hence regeneration into taller height classes (i.e. with reproductive individuals).

Recently, more studies have incorporated the effect of mesoherbivore browsing on vegetation dynamics. For example, impala were found to impact regeneration through seedling predation in Chobe National Park, Botswana (Moe et al. 2009). Using nursery grown seedlings, large herbivores (mainly impala) were found to affect seedling regeneration. However, the study was not designed to experimentally separate individual species effects of elephant, impala or other herbivores, and effects by impala were inferred from ungulate density counts in the area, rather than being specifically and exclusively tested.

Numerous studies have focused on megaherbivore impact on woody communities (Owen-Smith 1988; Ben-Shahar 1998; Birkett 2002; Shannon et al. 2008), and on the effects of herbivores in

general on community structure and composition (Burke 1997; Bergquist et al. 1999; Cadenasso et al. 2002; Merrill et al. 2003; Kraaij & Milton 2006; Levick & Rogers 2008). A few studies have focused on the relative impacts of different-size herbivores amongst grazers (Young et al. 2005; Cromsigt 2006), ungulates and rodents (Shaw et al. 2002; Goheen et al. 2004), or between sexually dimorphic individuals within species (Stokke & Du Toit 2002; Kirby et al. 2008). Exclosure studies to elucidate herbivory effects, and in particular those of elephant, are few (e.g. Kraaij & Milton 2006; Levick & Rogers 2008; Siebert & Eckhardt 2008). A well-known research exclosure programme is the Kenya Long-term Exclosure Experiment (Shaw et al. 2002; Goheen et al. 2004, 2007; Riginos & Young 2007). Here groups of similar-size herbivores were excluded, but this still confounds any conclusive species-specific effect. Disentangling species specific effects is crucial in areas subjected to active population management. Active management includes interventions such as population reductions, removals and introduction (Slotow et al. 2005; Van Aarde & Jackson 2007). The consequences of these measures, and thus the species specific effects, need to be considered prior to implementation, as these interventions can have profound effects on the persistence of the ecosystem.

### ***The South African context***

In South Africa, the concern of elephant impact on vegetation, due to the increasing elephant population, is especially profound and has resulted in a 'Scientific assessment of elephant for South Africa' (Scholes & Mennell 2008). This assessment was initiated to collate the current scientific knowledge on elephant to facilitate well-informed decisions for future elephant management within the country (Scholes & Mennell 2008). In addition, it specified key areas of urgent future research to be able to assist elephant management. Examples are the economics of elephant, self-regulation of elephant populations, and the effect of increasing elephant populations on biodiversity.

Most elephant populations in South Africa are now conserved within confined protected areas (Slotow et al. 2005; Van Aarde et al. 2008). Elephant impact is thus no longer dispersed over the landscape as historical migration routes are cut off by fences (Van Aarde et al. 2008). As populations increase, elephant effects on vegetation may be exacerbated (Kerley et al. 2008; Van Aarde et al. 2008). This may facilitate changes to ecological functioning within protected areas (Kerley et al. 2008; Kalwij et al. 2010).

One of the main concerns, besides the overall impact of elephant on ecosystems, is the decrease or absence of especially tall trees in conservation areas (Eckhardt et al. 2000; Kalwij et al. 2010). No study has quantified if tree size classes are indeed absent from the system. The absence of a certain size class within the population can cause a lag-effect in the transition into taller and mature height classes, which can affect recruitment (cf. Barnes 2001; Wilson & Witkowski 2003), and thus persistence of the species. It is not clear if lower densities in certain size classes (or the absence) are recruitment, or mortality, related. Recruitment is dependent on a multiplicity of factors, such as quantity and quality of seed production by parent trees and rainfall (Fenner & Thompson 2005). Mortality can be inflicted by climatic events (e.g. droughts), high intensity fires or herbivory (Midgley et al. 2010).

In South Africa, more studies have included browsing impact (i.e. foraging impact on woody vegetation) in the last decade (Bond & Loffell 2001; Wiseman et al. 2004; Levick & Rogers 2008; Shannon et al. 2008; Asner et al. 2009; Staver et al. 2009). However, most research has focussed on herbivore-fire interactions (Mills & Fey 2005; Mourik et al. 2007; Levick et al. 2009), and studies experimentally separating different-sized browsing herbivores have been absent. Also, the effect of landscape position on herbivory and vegetation structure has received scant attention. Many savanna areas in South Africa consist of distinct catenas (i.e. the hillslope gradient from crest to footslope) within the landscape (Ben-Shahar 1990; Scholes & Walker 1993; Khomo & Rogers 2005). The effect of grazers at the hillslope scale has been well studied (Macandza et al. 2004; Grant & Scholes 2006), but this is less so for browsers.

It becomes clear that there is a need to understand the specific species effects of different herbivores, their effect on tree size class distributions, but also to understand the effect of landscape on herbivory and vegetation. Therefore this dissertation focuses on the herbivory effect of both elephant and mesoherbivores. Study areas comprised savanna woodlands and the critically endangered Sand Forest, within the savanna and forest biome in South Africa.

### **The savanna biome**

The savanna biome is the largest biome in South Africa, covering over 33% of South Africa (Shackleton et al. 2007). Only 8% of the savannas are under conservation (Shackleton et al. 2007). Rainfall, nutrients (both primary determinants), fire and herbivores are the main drivers of savannas, which interactions maintain the characteristic codominance of trees and grasses defining the savanna system (Scholes & Walker 1993; Higgins et al. 2000). Mineralisation of

nutrients and primary production is determined by water availability, which increases with rainfall during the wet season (Scholes & Walker 1993). Rainfall increases woody cover and recruitment (Wilson & Witkowski 1998; Higgins et al. 2000). However, higher rainfall also stimulates grass biomass, which increases the fire intensity (Sankaran et al. 2008). Fire in turn improves the quality of vegetation regrowth, thus increasing herbivory in post-burn areas (Mourik et al. 2007). Although widespread, threats such as land transformations, climate change, inappropriate management (e.g. fire regimes and herbivore population dynamics) and over-utilisation by herbivores and man, may jeopardise the sustainability of savannas (Mucina & Rutherford 2006; Wigley et al. 2010). Being an important pool of biodiversity (Scholes & Walker 1993; Du Toit & Cumming 1999), the effects of different drivers on this system need to be fully understood.

### **The forest biome**

The smallest biome in South Africa is the forest biome, with only 0.1% of the land surface covered with indigenous forest (references in Mucina & Rutherford 2006). Sand Forest is a deciduous dry forest type restricted to the Maputaland Centre of Endemism in north-eastern South Africa and Mozambique (Kirkwood & Midgley 1999; Matthews et al. 2003; Siebert et al. 2004). Its restricted geographic range and unique species composition makes Sand Forest one of the most important habitat types for conservation in southern Africa (Moll 1980; Kirkwood & Midgley 1999; Matthews 2005). Sand Forest occurs in a mosaic of patches enclosed by mixed woodland or savanna bushveld (Matthews 2005; Kellerman & Van Rooyen 2007). The vegetation dynamics of the forest are poorly understood (Kellerman & Van Rooyen 2007), and the structural diversity in some protected areas has changed drastically over the past decade (W. Matthews, pers. comm.; K. Pretorius, pers. comm.), which coincided with an increase of elephant and nyala after (re)introductions of these species in the early 1990s (Druce et al. 2006; Repton 2007; Druce et al. 2008). Sand Forest is under threat of selective species utilisation by both man and herbivores, the effects of which are exacerbated by the forest's low resilience to disturbance, and poor recruitment rates of its tree species (Matthews et al. 2003; Botes et al. 2006; Gaugris et al. 2008). Foraging activities create pathways which open up the forest (Kerley et al. 2008; Shannon et al. 2009), which may allow savanna vegetation to enter these gaps. The consequent successive change to savanna woodland may be irreversible (Matthews 2005; Botes et al. 2006). It is thus likely that both elephant and nyala will have a substantial impact on the forest vegetation (Matthews et al. 2003; Repton 2007; Kirby et al. 2008).

*Elephant, impala, nyala and small-sized herbivores*

Elephant utilise both savanna woodlands and Sand Forest. Nyala prefer using Sand Forest when available, in contrast to impala which are mainly found in savanna woodlands (Estes 1991; Kirby et al. 2008; G. Lagendijk, pers. obs.). Impala are common in southern and eastern Africa (de Garine-Wichatitsky et al. 2004), while nyala populations are limited to southern Africa (Estes 1991). All three species are mixed feeders (species which feed on woody species as well as for which grass includes 10-90% of the diet (Fritz & Loison 2006)), generally meaning that grass is favoured in summer, while a diet switch towards browse takes place during winter (Estes 1992; Gagnon & Chew 2000; Fritz et al. 2002; Codron et al. 2007).

While impala have been linked to limitation of woody plant recruitment (Prins & van der Jeugd 1993; Skarpe et al. 2004), this has not yet been studied for nyala. The Sand Forest provides an excellent opportunity to study the effect of nyala on Sand Forest, as nyala is the only mesoherbivore utilising the Sand Forest in our study area. We managed here to experimentally separate the browsing effect between elephant and nyala through our enclosure experiment. Using an enclosure experiment provided us with the opportunity to explore the effects of browsing release by these species on vegetation composition and resource utilisation by small-size herbivores (i.e. common duiker, red duiker *Cephalophus natalensis*, and suni – all browsers). Impala are the most abundant mesoherbivore species with most of my savanna study areas (Owen-Smith & Ogutu, 2003; Repton 2007; C. Ferguson, pers. comm.; G. Lagendijk, pers. obs.), and were therefore expected to have the largest effect of all mesoherbivores on the savanna vegetation dynamics.

***Aim***

The general aim of this thesis is to expand our current understanding of the browsing of mega- and mesoherbivores, and the implications for woody vegetation, and other herbivore species, in order to provide a scientific framework to facilitate management decisions relating to herbivore species assemblages (i.e. composition and densities) within protected areas. More specifically, the dissertation aims to assess the role of elephant and mesoherbivores:

- 1) on woody vegetation communities, both in terms of structural diversity (i.e. different size and height classes) and species assemblages
- 2) on resource utilisation by their smaller counterparts.

***Thesis outline***

Savanna woodlands are the central focus in chapters 2 and 3. **Chapter 2** investigates if size classes are missing from the savanna ecosystem, or if densities vary within height classes across protected areas. This will contribute to the understanding of the effects of different drivers (e.g. rainfall, elephant and fire) on structural diversity within savannas.

In **Chapter 3** the importance of hillslope position and elephant for woody species assemblages and herbivory is determined. This study also allowed me to examine the effects of short-term elephant access to an area, contrary to most studies which study the effects of elephant exclusion.

Sand Forest is the focus of the studies presented in chapter 4 and 5. The Sand Forest studies provided the opportunity to experimentally separate a mega- (elephant) and mesoherbivores' (nyala) effect on the forest and other herbivores, using replicated exclosures. To my knowledge this is the first study to experimentally separate the effect between these two herbivores. In **chapter 4** I describe the role of elephant and nyala on Sand Forest recruitment, through their single and combined species browsing effect. While herbivory by megaherbivores has been well documented, the specific browsing effects of both a meso- and megaherbivore on recruitment remain largely unknown.

**Chapter 5** determines the effect of browsing release on tree species assemblages, and resource utilisation by a mesoherbivore and small-size herbivores. Identifying the effects of browsing release by different herbivores is especially relevant in highly managed protected areas, where manipulations of herbivore densities (e.g. population reductions, removal or introduction) are a well-used management tool.

In **chapter 6** the findings of these studies are synthesized. It attempts to provide insight into the effects (or impact) of mega- and mesoherbivores on vegetation within the savanna and forest biome, and to increase the understanding of the challenging conservation problems protected areas are facing while conserving high population densities of multi-herbivore species assemblages. Chapter 6 ends with concluding remarks regarding these issues and some suggestions for the way forward in conserving South African savannas and forests.

Note that for recruitment I use size classes based on limits at which levels of impact from different-size browsing herbivores can occur and that I thus not adhere to physiological seedlings and saplings.

### References

- Archibald, S.A., Roy, D.P., Van Wilgen, B.W. & Scholes, R.J. (2009) What limits fire? An examination of drivers of burnt area in Southern Africa. *Global Change Biology*, 15, 613-630.
- Asner, G.P., Levick, S., Kennedy-Bowdoin, T., Knapp, D.E., Emerson, R., Jacobson, J., Colgan, M.S. & Martin, R.E. (2009) Large-scale impacts of herbivores on the structural diversity of African savannas. *PNAS*, 106, 4947-4952.
- Barnes, M.E. (2001) Effects of large herbivores and fire on the regeneration of *Acacia erioloba* woodlands in Chobe National Park, Botswana. *African Journal of Ecology*, 39, 340-350.
- Belsky, A.J. (1984) Role of small browsing mammals in preventing woodland regeneration in the Serengeti National Park, Tanzania. *African Journal of Ecology*, 22, 271-279.
- Ben-Shahar, R. (1990) Soil nutrients distribution and moisture dynamics on upper catena in a semi-arid nature reserve. *Vegetatio*, 89, 69-77.
- Ben-Shahar, R. (1998) Changes in structure of savanna woodlands in northern Botswana following the impacts of elephants and fire. *Plant Ecology*, 136, 189-194.
- Bergquist, J., Örlander, G. & Nilsson, U. (1999) Deer browsing and slash removal affect field vegetation on south Swedish clearcuts. *Forest Ecology and Management*, 115, 171-182.
- Birkett, A. (2002) The impact of giraffe, rhino and elephant on the habitat of a black rhino sanctuary in Kenya. *African Journal of Ecology*, 40, 276-282.
- Bond, W.J. & Loffell, D. (2001) Introduction of giraffe changes acacia distribution in a South African savanna. *African Journal of Ecology*, 39, 286-294.
- Bond, W.J. & Archibald, S. (2003) Confronting complexity: fire policy choices in South African savanna parks. *International Journal of Wildland Fire*, 12, 381-389.
- Bond, W.J., Smythe, K.A. & Balfour, D.A. (2001) Acacia species turnover in space and time in an African savanna. *Journal of Biogeography*, 28, 117-128.
- Bork, E.W., Hudson, R.J. & Bailey, A.W. (1997) Populus forest characterization in Elk Island National Park relative to herbivory, prescribed fire, and topography. *Canadian Journal of Botany*, 75, 1518-1526.

- Botes, A., McGeoch, M.A. & Van Rensburg, B.J. (2006) Elephant- and human-induced changes to dung beetle (Coleoptera: Scarabaeidae) assemblages in the Maputaland Centre of Endemism. *Biological Conservation*, 130, 573-583.
- Bothma, J.D.P., van Rooyen, N. & van Rooyen, M.W. (2004) Using diet and plant resources to set wildlife stocking densities in African savannas. *Wildlife Society Bulletin*, 32, 840-851.
- Burke, A. (1997) The impact of large herbivores on floral composition and vegetation structure in the Naukluft Mountains, Namibia. *Biodiversity and Conservation*, 6, 1203-1217.
- Cadenasso, M.L., Pickett, S.T.A. & Morin, P.J. (2002) Experimental test of the role of mammalian herbivores on old field succession; community structure and seedling survival. *Journal of the Torrey Botanical Society*, 129, 228-237.
- Carruthers, J., Boshoff, A.F., Slotow, R., Biggs, H.C., Avery, G. & Matthews, W. (2008) The elephant in South Africa: history and distribution. *Elephant management: A scientific assessment for South Africa* (ed. by M.C. Scholes and K.G. Mennell), pp. 23-83. Wits University Press, Johannesburg.
- Castro, J., Zamora, R., Hódar, J.A. & Gómez, J.M. (2004) Seedling establishment of a boreal tree species (*Pinus sylvestris*) at its southernmost distribution limit: consequences of being in a marginal Mediterranean habitat. *Journal of Ecology*, 92, 266-277.
- Caughley, G. (1976) The elephant problem - an alternative hypothesis. *East African Wildlife Journal*, 14, 265-283.
- Chapin, F.S., Zavaleta, E.S., Eviner, V.T., Naylor‡, R.L., Vitousek, P.M., Reynolds, H.L., Hooper, D.U., Lavorel, S., Sala, O.E., Hobbie, S.E., Mack, M.C. & Díaz, S. (2000) Consequences of changing biodiversity. *Nature*, 405, 234-242.
- Clarke, J. & Grundy, I.M. (2004) The socio-economics of forest and woodland resource use. *Indigenous forests and woodlands in South Africa: Policy, people and practice* (ed. by M.J. Lawes, H.a.C. Eeley, C.M. Shackleton and B.G.S. Geach), pp. 167-193. University of KwaZulu-Natal Press, Scottsville.
- Codron, D., Codron, J., Lee-Thorp, J.A., Sponheimer, M., de Ruiter, D., Sealy, J., Grant, R. & Fourie, N. (2007) Diets of savanna ungulates from stable carbon isotope composition of faeces. *Journal of Zoology*, 273, 21-29.
- Cromsigt, J.P.G.M. (2006) *Large herbivores in space: resource partitioning among savanna grazers in a heterogeneous environment*. PhD, Rijksuniversiteit Groningen, Groningen.
- Danell, K., Bergström, R., Edenius, L. & Ericsson, G. (2003) Ungulates as drivers of tree population dynamics at module and genet levels. *Forest ecology and management*, 181, 67-76.

- de Garine-Wichatitsky, M., Fritz, H., Gordon, I.J. & Illius, A.W. (2004) Bush selection along foraging pathways by sympatric impala and greater kudu. *Oecologia*, 141, 66-75.
- De Graaff, M.-A., Van Groenigen, K.-J., Six, J., Hungate, B. & Van Kessel, C. (2006) Interactions between plant growth and soil nutrient cycling under elevated CO<sub>2</sub>: a meta-analysis. *Global Change Biology*, 12, 1-15.
- de Knegt, H.J., Groen, T.A., Van de Vijver, C.A.D.M., Prins, H.H.T. & Van Langevelde, F. (2008) Herbivores as architects of savannas: inducing and modifying spatial vegetation patterning. *Oikos*, 117, 543-554.
- Díaz, S. & Cabido, M. (2001) Vive la différence: plant functional diversity matters to ecosystem processes. *Trends in Ecology and Evolution*, 16, 646-655.
- Druce, H.C., Pretorius, K. & Slotow, R. (2008) The response of an elephant population to conservation area expansion: Phinda Private Game Reserve, South Africa. *Biological Conservation*, 141, 3127-3138.
- Druce, H.C., Pretorius, K., Druce, D. & Slotow, R. (2006) The effect of mature elephant bull introductions on ranging patterns of resident bulls: Phinda Private Game Reserve, South Africa. *Koedoe*, 49, 77-84.
- Du Toit, J.T. (2003) Large herbivores and savanna heterogeneity. *The Kruger Experience: Ecology and management of savanna heterogeneity* (ed. by J.T. Du Toit, K.H. Rogers and H.C. Biggs), pp. 292-309. Island Press, Washington.
- Du Toit, J.T. & Cumming, D.H.M. (1999) Functional significance of ungulate diversity in African savannas and the ecological implications of the spread of pastoralism. *Biodiversity and Conservation*, 8, 1643-1661.
- Eckhardt, H.C., van Wilgen, B.W. & Biggs, H.C. (2000) Trends in woody vegetation cover in the Kruger National Park, South Africa, between 1940 and 1998. *African Journal of Ecology*, 38, 108-115.
- Egoh, B., Reyers, B., Rouget, M., Bode, M. & Richardson, D.M. (2009) Spatial congruence between biodiversity and ecosystem services in South Africa. *Biological Conservation*, 142, 553-562.
- Estes, R.D. (1991) *The behavior guide to African mammals: including hoofed mammals, canivores, primates*. University of California Press, Berkeley.
- Fashing, P.J., Forrester, A., Scully, C. & Cords, M. (2004) Long-term tree population dynamics and their implications for the conservation of the Kakamega Forest, Kenya. *Biodiversity and Conservation*, 13, 753-771.

- Fenner, M. & Thompson, K. (2005) *The ecology of seeds*. Cambridge University Press, Cambridge.
- Fornara, D.A. (2005) *Ungulate browsing as an ecosystem process: browser-plant-soil interactions in a southern African savanna*. PhD, University of Pretoria, Pretoria.
- Fritz, H. & Loison, A. (2006) Large herbivores across biomes. *Large herbivore ecology, ecosystem dynamics and conservation* (ed. by K. Danell, R. Bergström, P. Duncan and J. Pastor), pp. 19-49. Cambridge University Press, Cambridge.
- Fritz, H., Duncan, P., Gordon, I.J. & Illius, A.W. (2002) Megaherbivores influence trophic guilds structure in African ungulate communities. *Oecologia*, 131, 620-625.
- Gagnon, M. & Chew, A.E. (2000) Dietary preferences in extant African bovidae. *Journal of Mammalogy*, 81, 490-511.
- Gardner, T.A. (2006) Tree-grass coexistence in the Brazilian cerrado: demographic consequences of environmental instability. *Journal of Biogeography*, 33, 448-463.
- Gaugris, J.Y., Van Rooyen, M.W. & Bothma, J.D.P. (2008) Growth rate of selected woody species in northern Maputaland, KwaZulu-Natal, South Africa. *South African Journal of Botany*, 74, 85-92.
- Gill, R.M.A. & Beardall, V. (2001) The impacts of deer on woodlands: the effects of browsing and seed dispersal on vegetation structure and composition. *Forestry*, 74, 209-218.
- Goheen, J.R., Keesing, F., Allan, B.F., Ogada, D. & Ostfeld, R.S. (2004) Net effects of large mammals on *Acacia* seedling survival in an African savanna. *Ecology*, 85, 1555-1561.
- Gordon, I.J., Hester, A.J. & Festa-Bianchet, M. (2004) The management of wild large herbivores to meet economic, conservation and environmental objectives. *Journal of Applied Ecology*, 41, 1021-1031.
- Grant, C.C. & Scholes, M.C. (2006) The importance of nutrient hot-spots in the conservation and management of large wild mammalian herbivores in semi-arid savannas. *Biological Conservation*, 130, 426-437.
- Grellmann, D. (2002) Plant responses to fertilization and exclusion of grazers on an arctic tundra heath. *Oikos*, 98, 190-204.
- Guldmond, R.A.R. & Van Aarde, J. (2007) The impact of elephants on plants and their community variables in South Africa's Maputaland. *African Journal of Ecology*, 45, 327-335.
- Guy, P.R. (1975) The daily food intake of the African elephant, *Loxodonta africana* Blumenbach, in Rhodesia. *Arnoldia Rhodesia*, 7, 1-5.

- Haddad, C.R., Honiball, A.S., Dippenaar-Schoeman, A.S., Slotow, R. & Van Rensburg, B.J. (2010) Spiders as potential indicators of elephant-induced habitat changes in endemic sand forest, Maputaland, South Africa. *African Journal of Ecology*, 48, 446-460.
- Higgins, S.I., Bond, W.J. & Trollope, W.S.W. (2000) Fire, resprouting and variability: a recipe for grass-tree coexistence in savanna. *Journal of Ecology*, 88, 213-229.
- Jachmann, H. & Croes, T. (1991) Effects of browsing by elephants on the *Combretum/Terminalia* woodland at the Nazinga Game Ranch, Burkina Faso, West Africa. *Biological Conservation*, 57, 13-24.
- Jones, C.G., Lawton, J.H. & Shachak, M. (1994) Organisms as ecosystem engineers. *Oikos*, 69, 373-386.
- Joppa, L.N., Loarie, S.R. & Pimm, S.L. (2008) On the protection of "protected areas". *PNAS*, 105, 6673-6678.
- Kalwij, J.M., de Boer, W.F., Mucina, L., Prins, H.H.T., Skarpe, C. & Winterbach, C. (2010) Tree cover and biomass increase in a southern African savanna despite growing elephant population. *Ecological Applications*, 20, 222-233.
- Kellerman, M.J.S. & Van Rooyen, M.W. (2007) Seasonal variation in soil seed bank size and species composition of selected habitat types in Maputaland, South Africa. *Bothalia*, 37, 249-258.
- Kerley, G.I.H., Landman, M., Kruger, L., Owen-Smith, N., Balfour, D., de Boer, W.F., Gaylard, A., Lindsay, K. & Slotow, R. (2008) Effects of elephants on ecosystems and biodiversity. *Elephant Management: A Scientific Assessment for South Africa* (ed. by R.J. Scholes, Mennell, K.G.), pp. 146-205. Witwatersrand University Press, Johannesburg.
- Khomo, L.M. & Rogers, K.H. (2005) Proposed mechanism for the origin of sodic patches in Kruger National Park, South Africa. *African Journal of Ecology*, 43, 29-34.
- Kirby, T., Shannon, G., Page, B. & Slotow, R. (2008) The influence of sexual dimorphisms on the foraging behaviour of the nyala *Tragelaphus angasii*. *Acta Zoologica Sinica*, 54, 561-568.
- Kirkwood, D. & Midgley, J.J. (1999) The floristics of Sand Forest in northern KwaZulu-Natal, South Africa. *Bothalia*, 29, 293-304.
- Kohi, E.M., de Boer, W.F., Slot, M., Van Wieren, S.E., Ferwerda, J.G., Grant, R.C., Heitkönig, I.M.A., de Knecht, H.J., Knox, N., Van Langevelde, F., Peel, M., Slotow, R., Van der Waal, C. & Prins, H.H.T. (2009) Effects of simulated browsing on growth and leaf chemical properties in *Colophospermum mopane* saplings. *African Journal of Ecology*, 48, 190-196.

- Kraaij, T. & Milton, S.J. (2006) Vegetation changes (1995-2004) in semi-arid Karoo shrubland, South Africa: Effects of rainfall, wild herbivores and change in land use. *Journal of Arid Environments*, 64, 174-192.
- Lagendijk, D.D.G., de Boer, W.F. & Van Wieren, S.E. (2005) Can African elephants survive and thrive in monostands of *Colophospermum mopane* woodlands? *Pachyderm*, 39, 43-49.
- Lawes, M.J., Midgley, J.J. & Chapman, C.A. (2004) South Africa's forests: The ecology and sustainable use of indigenous timber resources. *Indigenous forests and woodlands in South Africa: Policy, people and practice* (ed. by M.J. Lawes, H.a.C. Eeley, C.M. Shackleton and B.G.S. Geach), pp. 31-75. University of KwaZulu-Natal Press, Scottsville.
- Levick, S. & Rogers, K. (2008) Patch and species specific responses of savanna woody vegetation to browser exclusion. *Biological Conservation*, 141, 489-498.
- Levick, S., Asner, G.P., Kennedy-Bowdoin, T. & Knapp, D.E. (2009) The relative influence of fire and herbivory on savanna three-dimensional vegetation structure. *Biological Conservation*, 142, 1693-1700.
- Lewis, D.M. (1987) Fruiting patterns, seed germination, and distribution of *Sclerocarya caffra* in an elephant-inhabited woodland. *Biotropica*, 19, 50-56.
- Lykke, A.M. (1998) Assessment of species composition change in savanna vegetation by means of woody plants' size class distributions and local information. *Biodiversity and Conservation*, 7, 1261-1275.
- Macandza, V.A., Owen-Smith, N. & Cross, P.C. (2004) Forage selection by African buffalo in the late dry season in two landscapes. *South African Journal of Wildlife Research*, 34, 113-121.
- Manning, A.D., Fischer, J. & Lindenmayer, D.B. (2006) Scattered trees are keystone structures - Implications for conservation. *Biological Conservation*, 132, 311-321.
- Matthews, W.S. (2005) *Contributions to the ecology of Maputaland, southern Africa, with emphasis on Sand Forest*. PhD, University of Pretoria, Pretoria.
- Matthews, W.S., Van Wijk, A.E., Van Rooyen, N. & Botha, G.A. (2003) Vegetation of Tembe Elephant Park, Maputaland, South Africa. *South African Journal of Botany*, 67, 573-594.
- Melillo, J.M., McGuire, A.D., Kicklighter, D.W., Moore III, B., Vorosmarty, C.J. & Schloss, A.L. (1993) Global climate change and terrestrial net primary production. *Nature*, 363, 234-240.

- Merrill, E.H., Beyer, H.L., Jones, G.P. & McDaniel, G.W. (2003) Deciduous woodland conservation under heavy deer browsing on Devils Tower National Monument, USA. *Journal for Nature Conservation*, 10, 221-232.
- Midgley, J.J., Lawes, M.J. & Chamaillé-Jammes, S. (2010) Savanna woody plant dynamics: the role of fire and herbivory, separately and synergistically. *Australian Journal of Botany*, 58, 1-11.
- Miller, M.F. (1995) Acacia seed survival, seed germination and seedling growth following pod consumption by large herbivores and seed chewing by rodents. *African Journal of Ecology*, 33, 194-210.
- Mills, A.J. & Fey, M.V. (2005) Interactive response of herbivores, soils and vegetation to annual burning in a South African savanna. *Austral Ecology*, 30, 435-444.
- Mkanda, F.X. (1999) Drought as an analogue climate change scenario for prediction of potential impacts on Malawi's wildlife habitats. *Climate Research*, 12, 215-222.
- Moe, S.R., Rutina, L.P., Hytteborn, H. & Du Toit, J.T. (2009) What controls woodland regeneration after elephants have killed the big trees? *Journal of applied ecology*, 46, 223-230.
- Moll, E.J. (1980) Terrestrial plant ecology. *Studies on the ecology of Maputaland* (ed. by M.N. Bruton and K.H. Cooper), pp. 52-68. Rhodes University & The Natal Branch of the Wildlife Society of Southern Africa.
- Mourik, A.A., Van Langevelde, F., Van Tellinghen, E., Heitkönig, I.M.A. & Gaigher, I. (2007) Stability of wooded patches in a South African nutrient-poor grassland: do nutrients, fire or herbivores limit their expansion? *Journal of Tropical Ecology*, 23, 529-537.
- Mucina, L. & Rutherford, M.C. (2006) *The vegetation of South Africa, Lesotho and Swaziland*. South African National Biodiversity Institute, Pretoria.
- O'Connor, T.G., Goodman, P.S. & Clegg, B. (2007) A functional hypothesis of the threat of local extirpation of woody plant species by elephant in Africa. *Biological Conservation*, 136, 329-345.
- Obiri, J.A.F., Lawes, M.J. & Mukolwe, M. (2002) The dynamics and sustainable use of high-value tree species of the coastal Pondoland forests of the Eastern Cape Province, South Africa. *Forest Ecology and Management*, 166, 131-148.
- Owen-Smith, N. & Ogutu, J.O. (2003) Rainfall influences on ungulate population dynamics. *The Kruger Experience: Ecology and management of savanna heterogeneity* (ed. by J.T. Du Toit, K.H. Rogers and H.C. Biggs), pp. 310-331. Island Press, Washington.

- Owen-Smith, R.N. (1988) *Megaherbivores: the influence of very large body size on ecology*. Cambridge University Press, Cambridge.
- Pace, M.L., Cole, J.J., Carpenter, S.R. & Kitchell, J.F. (1999) Trophic cascades revealed in diverse ecosystems. *TREE*, 14, 483-488.
- Pickett, S.T.A., Cadenasso, M.L. & Benning, T.L. (2003) Biotic and abiotic variability as key determinants of savanna heterogeneity at multiple spatiotemporal scales. *The Kruger Experience: ecology and management of savanna heterogeneity* (ed. by J.T. Du Toit, K.H. Rogers and H.C. Biggs), pp. 22-40. Island Press, Washington.
- Power, M.E., Tilman, D., Estes, J.A., Menge, B.A., Bond, W.J., Mills, S., Daily, G., Castilla, J.C., Lubchenco, J. & Paine, R.T. (1996) Challenges in the quest for keystones. *BioScience*, 46, 609-620.
- Pretorius, Y., de Boer, W.F., Van der Waal, C., de Knecht, H.J., Grant, R.C., Knox, N.M., Kohi, E.M., Mwakiwa, E., Page, B.R., Peel, M.J.S., Skidmore, A.K., Slotow, R., Van Wieren, S.E. & Prins, H.H.T. (2011) Soil nutrient status determines how elephant utilize trees and shape environments. *Journal of Animal Ecology*, 80, 875-883.
- Prins, H.H.T. & van der Jeugd, H.P. (1993) Herbivore Population Crashes and Woodland Structure in East Africa. *Journal of Ecology*, 81, 305-314.
- Repton, M. (2007) *Vegetation utilisation by elephants in the Mkuze and Phinda Game Reserves*. MSc, University of KwaZulu-Natal, Durban.
- Riginos, C. & Young, T.P. (2007) Positive and negative effects of grass, cattle, and wild herbivores on *Acacia* saplings in an East African savanna. *Oecologia*, 153, 984-995.
- Ripple, W.J. & Beschta, R.L. (2007) Restoring Yellowstone's aspen with wolves. *Biological Conservation*, 138, 514-519.
- Russell, F.L. & Fowler, N.L. (2004) Effects of white-tailed deer on the population dynamics of acorns, seedlings and small saplings of *Quercus buckleyi*. *Plant Ecology*, 173, 59-72.
- Sankaran, M., Ratnam, J. & Hanan, N. (2008) Woody cover in African savannas: the role of resources, fire and herbivory. *Global Ecology and Biogeography*, 17, 236-245.
- Sankaran, M., Hanan, N.P., Scholes, R.J., Ratnam, J., Augustine, D.J., Cade, B.S., Gignoux, J., Higgins, S.I., Le Roux, X., Ludwig, F., Ardo, J., Banyikwa, F., Bronn, A., Bucini, G., Caylor, K.K., Coughenour, M.B., Diouf, A., Ekaya, W., Feral, C.J., February, E.C., Frost, P.G.H., Hiernaux, P., Hrabar, H., Metzger, K.L., Prins, H.H.T., Ringrose, S., Sea, W., Tews, J., Worden, J. & Zambatis, N. (2005) Determinants of woody cover in African savannas. *Nature*, 438, 846-849.

- Scholes, R.J. & Walker, B.H. (1993) *An African savanna: synthesis of the Nylsvlei study*. Cambridge University Press.
- Scholes, R.J. & Mennell, K.G. (2008) *Elephant management: a scientific assessment for South Africa*. Wits University Press, Johannesburg.
- Shackleton, C.M. & Scholes, R.J. (2011) Above ground woody community attributes, biomass and carbon stocks along a rainfall gradient in the savannas of the central lowveld, South Africa. *South African Journal of Botany*, 77, 184-192.
- Shackleton, C.M., Shackleton, S.E., Buiten, E. & Bird, N. (2007) The importance of dry woodlands and forests in rural livelihoods and poverty alleviation in South Africa *Forest Policy and Economics*, 9, 558-577.
- Shannon, G., Matthews, W.S., Page, B.R., Parker, G.E. & Smith, R.J. (2009) The affects of artificial water availability on large herbivore ranging patterns in savanna habitats: a new approach based on modelling elephant path distributions. *Diversity and Distributions*, 15, 776-783.
- Shannon, G., Druce, D.J., Page, B.R., Eckhardt, H.C., Grant, R. & Slotow, R. (2008) The utilization of large savanna trees by elephant in southern Kruger National Park. *Journal of Tropical Ecology*, 24, 281-289.
- Shaw, M.T., Keesing, F. & Ostfeld, R.S. (2002) Herbivory on Acacia seedlings in an East African savanna. *Oikos*, 98, 385-392.
- Siebert, F. & Eckhardt, H.C. (2008) The vegetation and floristics of the Nkhuflu exclosures, Kruger National Park. *Koedoe*, 50, 126-144.
- Siebert, S.J., Fish, L., Uiras, M.M. & Izidine, S.A. (2004) Grass assemblages and diversity of conservation areas on the coastal plain south of Maputo Bay, Mozambique. *Bothalia*, 34, 61-71.
- Skarpe, C., Aarrestad, P.A., Andreassen, H.P., Dhillion, S.S., Dimakatso, T., Du Toit, J.T., Duncan, Halley, J., Hytteborn, H., Makhabu, S., Mari, M., Marokane, W., Masunga, G., modise, D., Moe, S.R., Mojaphoko, R., Mosugelo, D., Motsumi, S., Neo-Mahupeleng, G., Ramotadima, M., Rutina, L., Sechele, L., Sejoe, T.B., Stokke, S., swenson, J.E., Taolo, C., Vandewalle, M. & Wegge, P. (2004) The return of the giants: ecological effects of an increasing elephant population. *Ambio*, 33, 276-282.
- Slotow, R., Garaï, M.E., Reilly, B., Page, B. & Carr, R.D. (2005) Population dynamics of elephants re-introduced to small fenced reserves in South Africa. *South African Journal of Wildlife Research*, 35, 23-32.

- Staver, A.C., Bond, W.J., Stock, W.D., Jansen van Rensburg, S. & Waldram, M.S. (2009) Browsing and fire interact to suppress tree density in an African savanna. *Ecological Applications*, 19, 1909-1919.
- Stokke, S. & Du Toit, J.T. (2002) Sexual segregation in habitat use by elephants in Chobe National Park. *African Journal of Ecology*, 40, 360-371.
- Taylor, A.H. (2010) Fire disturbance and forest structure in an old-growth *Pinus ponderosa* forest, southern Cascades, USA. *Journal of Vegetation Science*, 21, 561-572.
- Van Aarde, R.J. & Jackson, T.P. (2007) Megaparks for metapopulations: Addressing the causes of locally high elephant numbers in southern Africa. *Biological Conservation*, 134, 289-297.
- Van Aarde, R.J., Ferreira, S.M., Jackson, T.P., Page, B., de Beer, Y., Gouch, K., Guldmond, R., Junker, J., Olivier, P., Ott, T. & Trimble, M. (2008) Elephant population biology and ecology. *Elephant management: A scientific assessment for South Africa* (ed. by M.C. Scholes and K.G. Mennell), pp. 84-145. Wits University Press, Johannesburg.
- van Wilgen, B.W., Govender, N., Biggs, H.C., Ntsala, D. & Funda, X.N. (2004) Response of savanna fire regimes to changing fire-management policies in a large African National Park. *Conservation Biology*, 18, 1533-1540.
- Vanak, A.T., Shannon, G., Thaker, M., Page, B., Grant, R. & Slotow, R. (2011) Biocomplexity in large tree mortality: interaction between elephant, fire and landscape in an African savanna. *Ecography*: doi: 10.1111/j.1600-0587.2011.07213.x
- Walker, B.H., Stone, L., Henderson, L. & Venede, M. (1986) Size structure analysis of the dominant trees in a South African savanna. *South African Journal of Botany*, 52, 397-402.
- Wigley, B.J., Bond, W.J. & Hoffman, M.T. (2010) Thicket expansion in a South African savanna under divergent land use: local vs. global drivers? *Global Change Biology*, 16, 964-976.
- Williams-Linera, G. & Lorea, F. (2009) Tree species diversity driven by environmental and anthropogenic factors in tropical dry forest fragments of central Veracruz, Mexico. *Biodiversity and Conservation*, 18, 3269-3293.
- Wilson, B.G. & Witkowski, E.T.F. (2003) Seed banks, bark thickness and change in age and size structure (1978-1999) of the African savanna tree, *Burkea africana*. *Plant Ecology*, 167, 151-162.
- Wilson, T.B. & Witkowski, E.T.F. (1998) Water requirements for germination and early seedling establishment in four African savanna woody plant species. *Journal of arid environments*, 38, 541-550.

- Wiseman, R., Page, B.R. & O'Connor, T.G. (2004) Woody vegetation change in response to browsing in Ithala Game Reserve, South Africa. *South African Journal of Wildlife Research*, 34, 25-37.
- Young, T.P., Palmer, T.M. & Gadd, M.E. (2005) Competition and compensation among cattle, zebras, and elephants in a semi-arid savanna in Laikipia, Kenya. *Biological Conservation*, 122, 351-359.

## **CHAPTER 2**

### **Rainfall, Elephant and Fire affect Height Class Distributions of Woody Vegetation in South African Savannas at Multiple Spatial Scales**

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**ABSTRACT**

**Aim** To determine which and how local and regional drivers affect the distribution of woody densities within different height classes, and whether size classes are absent from savannas.

**Location** South African savannas

**Methods** Using vegetation transect data, we conducted a meta-analysis to determine differences in woody densities within height classes across seven protected areas which differ in rainfall, fire return period, and time elapsed since elephant (re)introduction and elephant density.

**Results** Woody densities differed across reserves, and per functional height class. Size classes were absent from > 18 % of species in each reserve. Woody density was negatively affected by elephant exposure time, but was positively affected by elephant density, fire return period and especially by rainfall. Examining functional height classes, rainfall negatively affected large trees, but positively affected seedling and sapling densities. Densities of seedlings, medium and large trees all increased with longer fire return period. Elephant densities negatively affected seedlings, and elephant exposure time had a negative effect on seedlings, medium and large trees.

**Main conclusions** Disruptions in tree size distributions appear mortality related by drivers which can be actively manipulated by reserve management (i.e. elephant and fire). However, the contrasting effects of different drivers on structural diversity within savannas, and species specific responses, emphasise the need to monitor changes in vegetation at both the regional and reserve scale. This is necessary to be able to respond to changing levels or densities of drivers in order to conserve biodiversity across multiple scales.

**Key words:** Africa; disturbance; indicator species; Kruger National Park; recruitment; savanna woodlands; spatial scale; structure; size classes; tree densities;

## INTRODUCTION

At the global scale, woody thickening or bush encroachment is expanding (Wigley *et al.*, 2010). Increased levels of atmospheric carbon dioxide may promote this woody plant growth, acting as a global driver of ecosystem change (Wigley *et al.*, 2010). Savannas are dynamic ecosystems (Skarpe, 1992; Staver *et al.*, 2009), characterised by the coexistence of grass and trees (Higgins *et al.*, 2000), which cover 40% of Africa (Scholes & Walker, 1993). The high spatial heterogeneity of savanna allows for the highest large herbivore diversity on earth (Du Toit, 2003), illustrating their importance for conservation. Woody thickening potentially causes a biome shift from savanna to forest (Bond *et al.*, 2005; Wigley *et al.*, 2010). Changes to the current dynamic state of savannas will thus potentially involve loss of biota (e.g. savanna species replaced by forest species), with subsequent changes in ecosystem functioning (cf. Chapin *et al.*, 2000), as well as threatening the livelihoods of people which have an extensive historical coexistence with savanna (Du Toit & Cumming, 1999).

While savanna is becoming encroached at the global scale, quite the opposite is of concern at the regional and local scales. One of the current key questions in savanna ecology is what causes the decrease or loss of, especially large, trees (Eckhardt *et al.*, 2000; Kalwij *et al.*, 2010). The absence of trees within certain height classes may reflect a disruption within the ‘natural’ tree size distribution, or population dynamics (Walker *et al.*, 1986). But more importantly, the loss of one tree size class can cause a lag-effect in the transition of trees into taller size classes, or, in the absence of larger trees, even inhibit recruitment as reproductive individuals are absent (cf. Barnes, 2001; Wilson & Witkowski, 2003). This could potentially lead to local extinction of species, thereby ultimately affecting ecosystem functioning.

Three main ecological drivers of savanna dynamics are, at the regional scale, rainfall, and at the local scale, fire and herbivory (Scholes & Walker, 1993; Wigley *et al.*, 2010). Rainfall generally increases woody cover and recruitment (Higgins *et al.*, 2000; Kraaij & Ward, 2006). The loss of tree cover on the other hand is more often associated with the disturbance factors of fire and herbivory (Eckhardt *et al.*, 2000; Levick *et al.*, 2009; Staver *et al.*, 2009). Natural and anthropogenic fires are an integral component of the savanna system (Bond & Keeley, 2005). Fires reduce recruitment and height of trees. Trees below 3 m are susceptible to being retained within the fire-trap, unable to grow taller in the presence of fire (Bond *et al.*, 2001; Bond & Archibald, 2003; Levick *et al.*, 2009, but see Shannon *et al.*, 2008 for fire effects on larger trees). Fire thus affects the population demography by preventing the transition of individuals into taller

height classes (Bond & Archibald, 2003; Bond & Keeley, 2005). Fire is also called the ‘super-herbivore’ showing similarities to herbivory effects on vegetation, with the main difference that fire also affects unpalatable plants (Van de Koppel & Prins, 1998; Bond & Keeley, 2005). Browsing herbivores affect woody vegetation through their foraging activities, impacting on trees in different life stages. Medium-sized herbivores, such as nyala *Tragelaphus angasii* and impala *Aepyceros melampus*, inhibit recruitment (Moe *et al.*, 2009; Lagendijk *et al.*, 2011). Seedlings and saplings will have to escape a ‘browsing trap’ before being able to recruit into taller height classes (Bond & Archibald, 2003; Moe *et al.*, 2009; Lagendijk *et al.*, 2011). Conversely, elephant *Loxodonta africana* can kill even the largest mature trees by ring barking or pushing them over (Owen-Smith, 1988; Kerley *et al.*, 2008). As a result, the increase in elephant numbers in protected areas is of concern for the sustainability of savannas (Kalwij *et al.*, 2010). Beside elephant effects on structural diversity in woodlands, there are strong negative effects of small- and mesobrowsers on the smaller size classes (i.e. recruitment: seedlings and saplings) (Barnes, 2001; Moe *et al.*, 2009; Lagendijk *et al.*, 2011).

Although disturbances such as fire and herbivory are intrinsic to savanna systems, active management, and thus the capacity to manipulate these drivers, is common practice in protected areas (Bond & Archibald, 2003; Van Wilgen *et al.*, 2004; Slotow *et al.*, 2005). This, together with the current concerns regarding the effects of high elephant densities on vegetation (Kalwij *et al.*, 2010) requires understanding which drivers are influencing tree size distributions. We need to understand if disruptions in tree size distributions (i.e. the absence of size classes or classes with relatively low densities) are recruitment or mortality related in order to manage for the resilience to disturbances within savannas, and thus ultimately preservation of the savanna biome.

Conservation is driven at the local reserve level to regional/global scales through (inter)national laws and conventions. Broad-scale studies are few and often focus on woody cover (Sankaran *et al.*, 2005; Bucini & Hanan, 2007), while not taking into account densities in different life stages or size classes of woody vegetation. Furthermore, broad-scale studies may fail to detect local variation at smaller spatial scales. We here examined woody vegetation at both the reserve and regional level, including a more in-depth analysis of the population size distribution. In this way, we attempt to identify broad patterns across the regional scale, but at the same time take into account local variability at the reserve scale.

In this study, we examined woody vegetation within and across protected areas to understand which drivers are affecting the distribution of woody densities within different height classes. Specifically, in this paper we examine if (i) overall tree densities and densities per height class differ across protected areas, and (ii) the effect of resource availability (i.e. rainfall) and disturbance (*i.e.* elephant and fire) on tree abundance. We further examine (iii) if size classes are absent from these savanna areas. In addition (iv) we determine the effects of these factors on a number of tree species in more detail, as identifying species specific responses is vital in terms of ecosystem functioning and biodiversity conservation. Furthermore, (v) we assess indicator species which could potentially be used in large scale monitoring programmes to detect changes in savanna dynamics, as well as to determine effects from management interventions at the local scale. To our knowledge, this is the first study presenting a meta-analysis of tree densities across height classes.

## **METHODS**

Between 2000 and 2006, we collected woody vegetation data along transects in seven different protected savanna areas in South Africa (Table 1). In-depth descriptions of the study areas can be found in Kettles & Slotow (2009: Greater Makalali Private Game Reserve; hereafter Makalali), Mulqueeny *et al.* (2010: Mkuze), Trinkel *et al.* (2010: Madikwe), Macandza *et al.* (2004: central section Kruger), Druce *et al.* (2008: Phinda), Slotow *et al.* (2001: Pilanesberg) and Shannon *et al.* (2006: Pongola).

### **Woody vegetation sampling**

The woody vegetation was sampled using a lay-out consisting of three transects. For the first transect a 50 m tape was laid out at a random site. Transect 1 (2 x 50 m) in which only seedlings ( $\leq 0.5$  m) were recorded was nested within transect 2 (30 x 50 m) where individuals  $> 0.5$  m were recorded, which was nested within transect 3 (50 x 100 m) where individuals of additional species (*i.e.*, species not encountered in either transect (1) or (2)) were recorded, including all height classes. The underlined numbers could vary, as transect size was dependent on vegetation density and composition, with a minimum size such that all species and sufficient numbers within the range of height classes were recorded at each site. This sampling design is similar to Kalwij *et al.* (2010). In each transect, all individuals appropriate to the particular transect were counted, identified to species (Appendix S2.1) and height recorded. Heights of trees to 2 m were measured, and the heights of trees  $\geq 2$  m were estimated using the height of an observer as a scale following

**Table 1** Characteristics of the seven conservation areas included in the analyses

Reserve	GPS location Reserve	Size (km <sup>2</sup> )	First elephant introduction	Elephant density (/km <sup>2</sup> ) <sup>1</sup>	Fire return period (years)	Mean annual rainfall (mm)	Woody sampling year	Number of transects	Number of plant species recorded
Kruger National Park <sup>2</sup>	24°17' -36' S, 31°28' -58' E	19485	Already present in 1926	0.68	4.5	550 (central area)	'05-'06	56	86
Madikwe Game Reserve <sup>3</sup>	24°68' -87' S, 26°14' -47' E	615	1992	0.63	4.9	520	'00	111	72
Greater Makalali Private Game Reserve <sup>4</sup>	24°2'-13' S, 30°31'-46' E	218	1994	0.25	71.7	450	'02-'04	52	86
Mkuze Game Reserve <sup>5</sup>	27°33' -48' S, 32°06' -26' E	237	1994	0.13	5	700	'01-'02	95	140
Phinda Private Game Reserve <sup>6</sup>	27°40' -55' S, 32°12' -26' E	227	1992	0.45	7.4	764	'01-'02	59	144
Pilanesberg National Park <sup>7</sup>	25°22' -80' S, 26°57' -27°13' E	481	1981	0.24	2.5	630	'01-'02	150	110
Pongola Game Reserve <sup>8</sup>	27°54' -35' S, 31°86'-32°01' E	74	1997	0.41	5	500	'01-'02	42	83

<sup>1</sup> Elephant density year preceding vegetation sampling + 7% population growth

Data sources: <sup>2</sup> Macandza *et al.* (2004), Van Wilgen *et al.* (2000); <sup>3</sup> Trinkel *et al.* (2010), P. Nel, pers. comm.; <sup>4</sup> Delsink (2006), Druce (2000), A. Delsink, pers. comm.; <sup>5</sup> Mulqueeny *et al.* (2010), Ezemvelo KwaZulu-Natal Wildlife; <sup>6</sup> Morgan *et al.* (2009), S. Naylor, pers. comm.; <sup>7</sup> Moolman (2007), P. Nel, pers. comm.; <sup>8</sup> Shannon *et al.* (2006) Dr. H. Kohrs, pers. comm., H. Zitzer, pers. comm.

Shannon *et al.* (2008). In Pilanesberg, only one transect was sampled in which all woody trees of all sizes were recorded (transect area of  $\pm 250 \text{ m}^2$  each).

### **Data-analyses**

Because the concern about missing size classes is also related to herbivore impact, we allocated woody individuals to five functional height classes, which roughly correspond to the escape heights of impacts from different-size browsing herbivores in savannas. Following Legendijk *et al.* (2011), the classes we used are seedling ( $\geq 0.02\text{m}$  and  $\leq 0.5 \text{ m}$ ), sapling (0.51 - 1.5 m), small tree (1.51 - 3 m), medium tree (3.01 - 5 m) and large tree ( $> 5.01 \text{ m}$ ). Tree densities within each height class and overall were standardised to 1 ha. All tree species were included in the analyses, unless stated otherwise (see Table 1 for number of tree species included in each reserve).

Overall tree densities (i.e. all height classes combined) were log-transformed to meet assumptions of normality, and were tested for density differences among reserves using ANOVA. Differences in densities in each of the five functional height classes were tested among reserves using Kruskal-Wallis, as data were not normally distributed.

We also analysed the effect of elephant densities, time since elephant (re)introduction, fire return period and mean annual rainfall, on tree height classes. Elephant densities were calculated as the number of elephants present the year preceding the vegetation monitoring plus a 7% annual population increase (see Mackey *et al.*, 2006) (Table 1).

The fire return periods since elephant introduction were either obtained from the literature or calculated from data received from the reserve managers (Table 1), as

$$RP = \frac{(y)}{(b/a)}$$

Where  $RP$  is the fire return period in years,  $y$  is the number of years in which fire occurrence (or absence) was recorded,  $b$  is the total area burnt during  $y$ , and  $a$  is the total area of the reserve (Van Wilgen *et al.*, 2000).

Backwards regression models were used to identify explanatory variables (i.e. elephant density, time since elephant introduction, mean annual rainfall and fire return period), affecting overall densities across reserves. The assumptions of parametric multiple regression were violated for

densities per functional height class, we therefore calculated Spearman's rank correlations as a non-parametric alternative for these more focussed analyses. Transects were treated as independent from each other within reserves. Pseudoreplication may be of concern when analysing data in this way, however we believed it important to retain the variation among transects within reserves because the drivers are heterogeneous within reserves, even though they are applied as consistent factors for a reserve.

Tree populations are typically regenerating when the population structure displays an inverse J-shaped frequency distribution (Lykke, 1998, Obiri *et al.*, 2002), with a relatively high abundance of seedlings (*i.e.* recruitment) and a relatively low abundance of large trees. Population structures are more conventionally analysed using diameter size classes (Lykke, 1998, Obiri *et al.*, 2002). But given our interest in vertical structural patterns, we analysed height class distributions (HCD), which reflect population structures, for each of these seven reserves using linear regression (cf. Legendijk *et al.*, 2011, Lykke, 1998, Condit *et al.*, 1998). Data were pooled per reserve, and the number of individual trees per height class was divided by the width of the height class, to give an average density ( $D_i$ ) for the class midpoint ( $M_i$ ). To transform the non-linear inverse J-shaped curve to a linear form,  $D_i$  and  $M_i$  were 'ln + 1' – transformed prior to regression analyses. An inverse J-shaped curve is represented by a steep negative slope, while species with little regeneration show a negative slope close to zero.

To determine if size classes were missing from reserves species within each reserve were assessed for missing height classes up to the maximum height a specific species could attain (Coates Palgrave, 2002). We here made the assumption that species have the capacity to reach this maximum height in each of the seven reserves. To exclude the effect of rare species on missing size classes, only species which on average occurred with ten or more individuals per ha were included in the analysis. Per reserve, we expressed the number of species with individuals missing in a particular size class in which it should occur, as a percentage of all species that should occur within that size class.

Species are expected to respond differently to disturbance. Therefore the effects of the four variables on overall densities and height classes were further determined for the twelve tree species which occurred in all seven reserves (Appendix S2.2), using backwards regression models. Eleven of these twelve species have the potential to grow into large trees (*i.e.* > 5 m); *Gymnosporia senegalensis* reaches only the medium height class (*i.e.* 3 – 5 m tall).

Only significant regression models were reported. All analyses were run in PASW Statistics 18.0.2 (PASW Inc., Chicago, IL, U.S.A.).

## RESULTS

### Effects at the regional scale

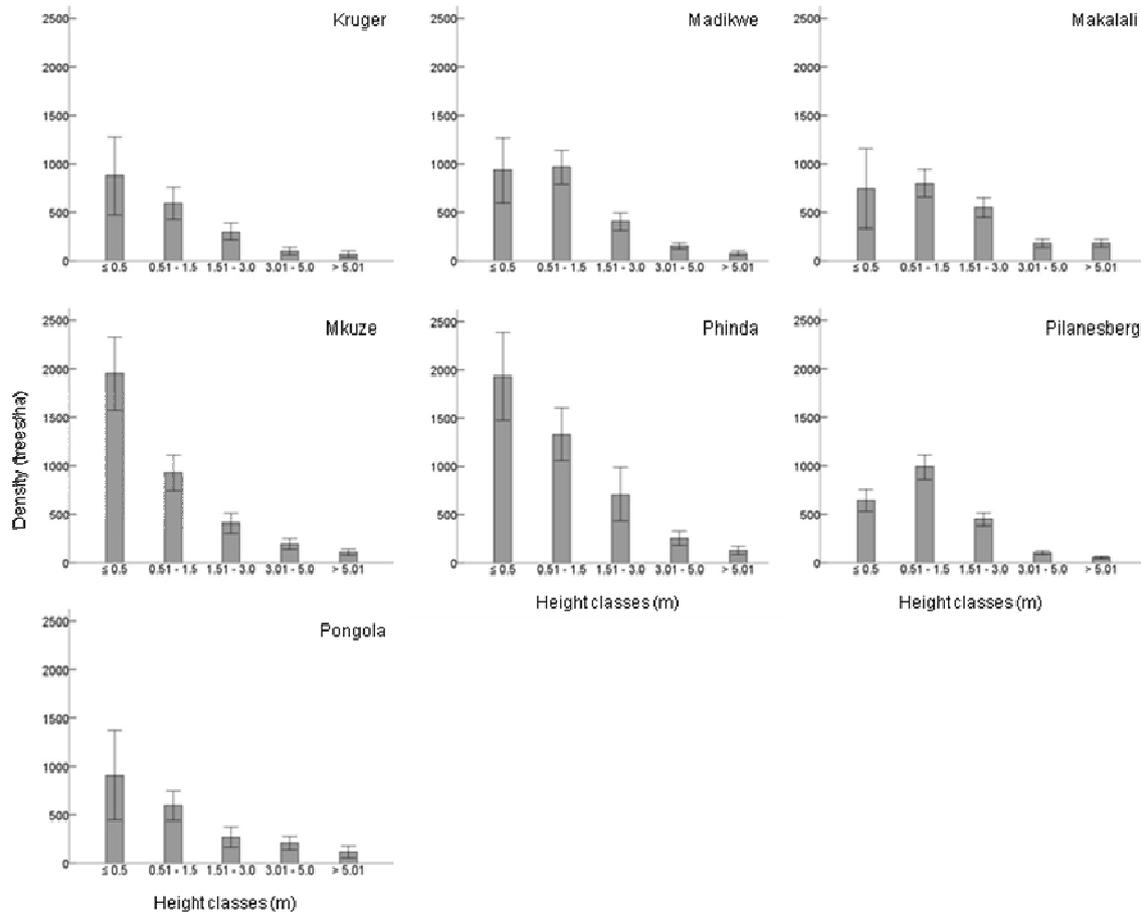
Overall tree densities (*i.e.* all height classes and species included) were significantly different among reserves ( $F_{1,6} = 10.997$ ,  $P < 0.001$ ). Seedling and sapling densities differed significantly among reserves (seedling:  $\chi^2_6 = 111.898$ ,  $P < 0.001$ ; sapling:  $\chi^2_6 = 42.717$ ,  $P < 0.001$ ; Fig. 1). Small, medium and large tree densities were each also significantly different among reserves ( $P < 0.001$ ; Fig.1).

Variation in the total tree densities among reserves was best, but weakly, explained by the backwards regression model including all variables, *i.e.* time since elephant introduction, elephant density, rainfall and fire return period ( $F_{4,560} = 15.626$ ,  $P < 0.001$ ,  $R^2 = 0.094$ ; Fig. 2). Total tree densities decreased with longer time since elephant introduction ( $\beta = -0.143$ ,  $t = -3.231$ ,  $P = 0.001$ ; Fig. 2). There was a positive effect of elephant density ( $\beta = 0.109$ ,  $t = 2.019$ ,  $P = 0.044$ ), fire return period ( $\beta = 0.211$ ,  $t = 4.023$ ,  $P < 0.001$ ), and most strongly of rainfall ( $\beta = 0.360$ ,  $t = 6.340$ ,  $P < 0.001$ ; Fig. 2), on total tree densities.

When height classes were analysed separately however, there was a significant negative effect of time since elephant introduction on seedlings ( $r_s = -0.193$ ,  $P < 0.001$ ), medium ( $r_s = -0.173$ ,  $P < 0.001$ ) and large trees ( $r_s = -0.182$ ,  $P < 0.001$ ; Table 2, Fig. 3). Elephant densities only negatively affected seedling densities ( $r_s = -0.196$ ,  $P < 0.001$ ; Table 2, Fig. 3). Fire return period had a positive effect on seedlings ( $r_s = 0.255$ ,  $P < 0.001$ ), medium ( $r_s = 0.224$ ,  $P < 0.001$ ) and large trees ( $r_s = 0.298$ ,  $P < 0.001$ ; Table 2, Fig. 3). Rainfall showed a negative correlation with large trees ( $r_s = -0.103$ ,  $P = 0.014$ ), but showed a positive effect on seedlings ( $r_s = 0.352$ ,  $P < 0.001$ ) and saplings ( $r_s = 0.151$ ,  $P < 0.001$ ; Table 2, Fig. 3).

### Effects at the reserve scale

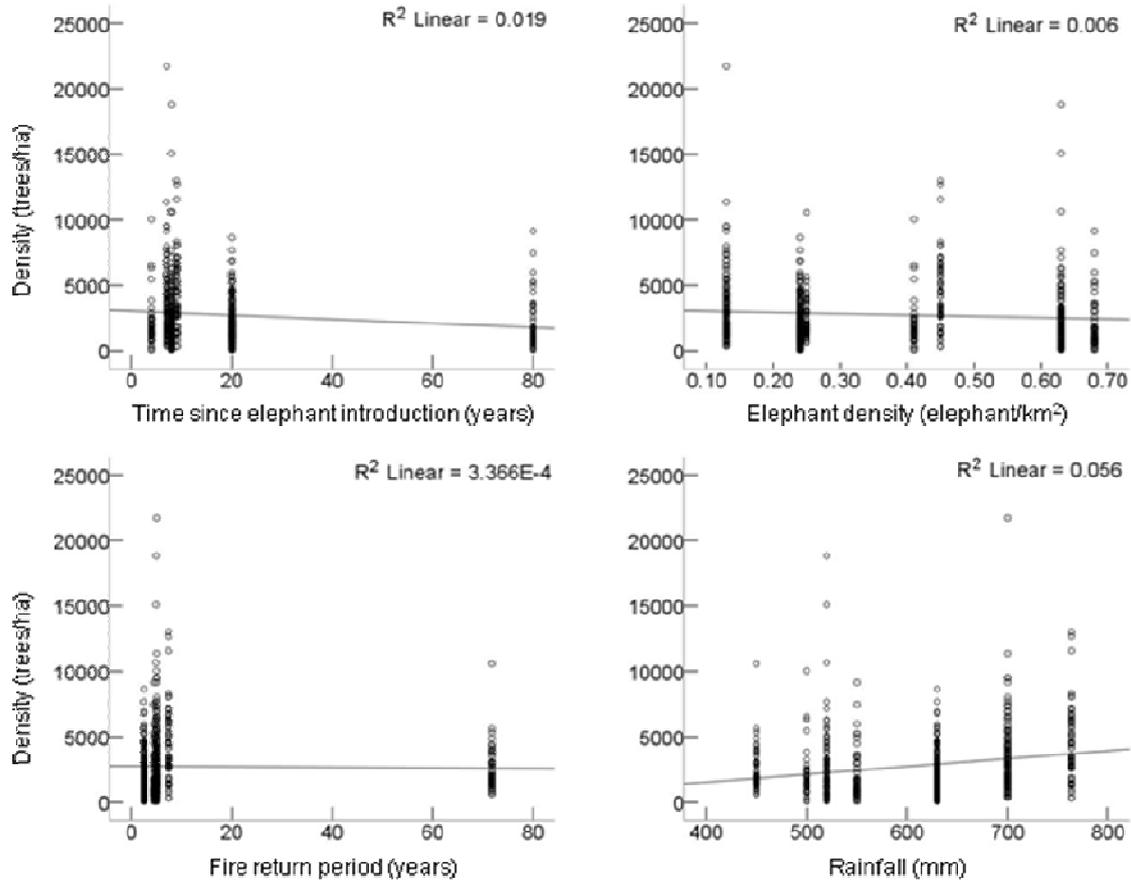
The height class distributions including all species were variable among reserves (Fig. 1). The distributions of Mkuze and Phinda each showed a clear inverse J-shaped curve, with Pongola and Kruger approaching this. However, both Pilanesberg and Kruger had relatively few large trees.



**Figure 1** Height class distributions per reserve including all species. The bars indicate 95% confidence intervals of the means.

Pilanesberg harboured more saplings than seedlings, which was also the case, but in a lesser extent, in Madikwe and Makalali. However all reserves showed a strong negative HCD slope (Fig. 4), indicating that, despite the reduced densities in the smallest size class in Madikwe, Makalali and Pilanesberg, all reserves were recruiting individuals through the height classes.

Size classes were missing from even the more abundant species within each reserve (Table 3). In Madikwe, only 18.2 % of 33 species had individuals missing from one or more functional height classes, while in all other reserves, more than 30% of species had height classes missing from the population structure (the most in Pongola, with 51.7 % of species missing a height class).



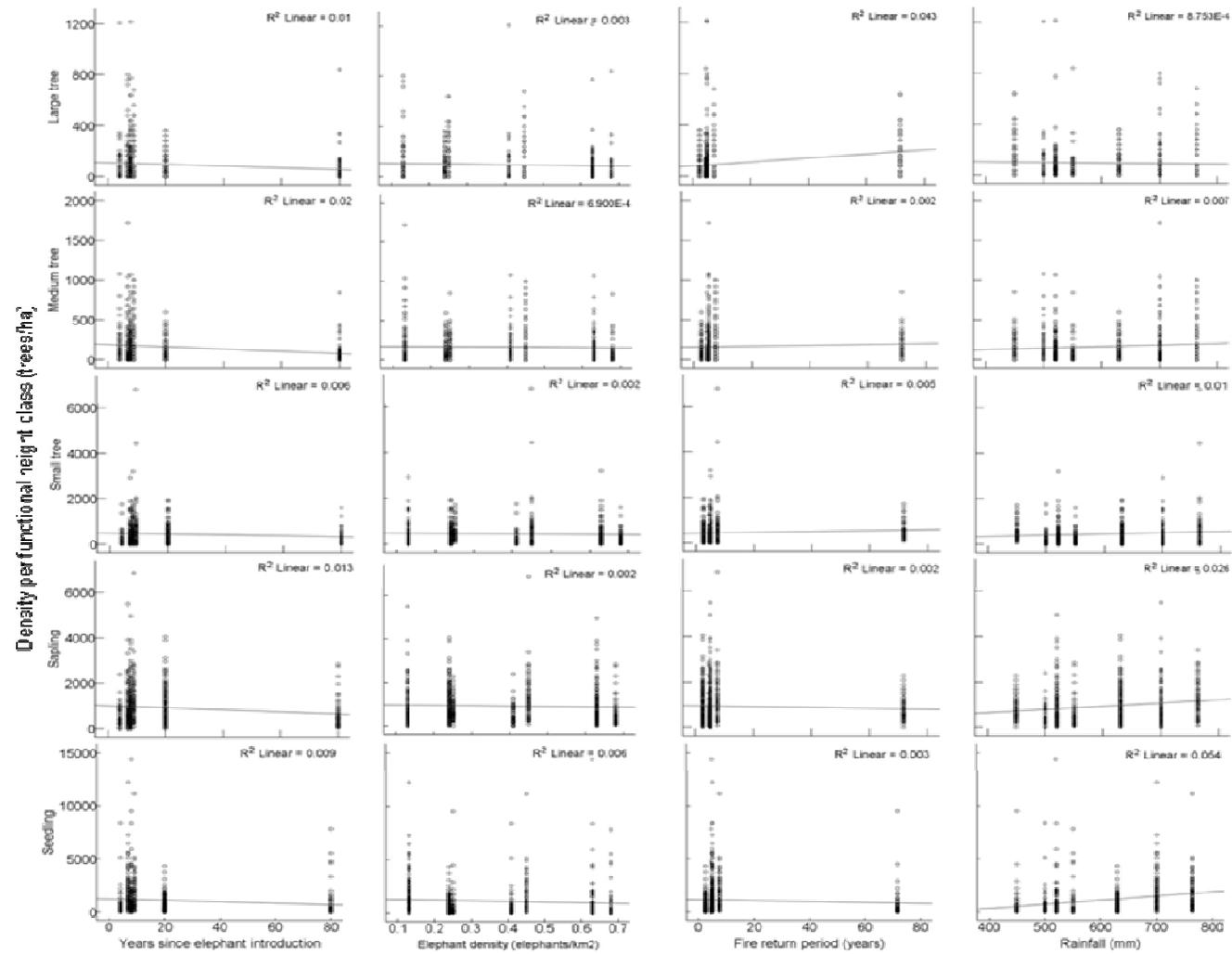
**Figure 2** Effects of time since elephant introduction, elephant density, fire return period and mean annual rainfall on overall tree densities (*i.e.* all size classes included) across seven reserves (N = 565).

**Table 2** Spearman correlation coefficients for tree densities vs. time since elephant introduction, elephant densities, fire return period and rainfall

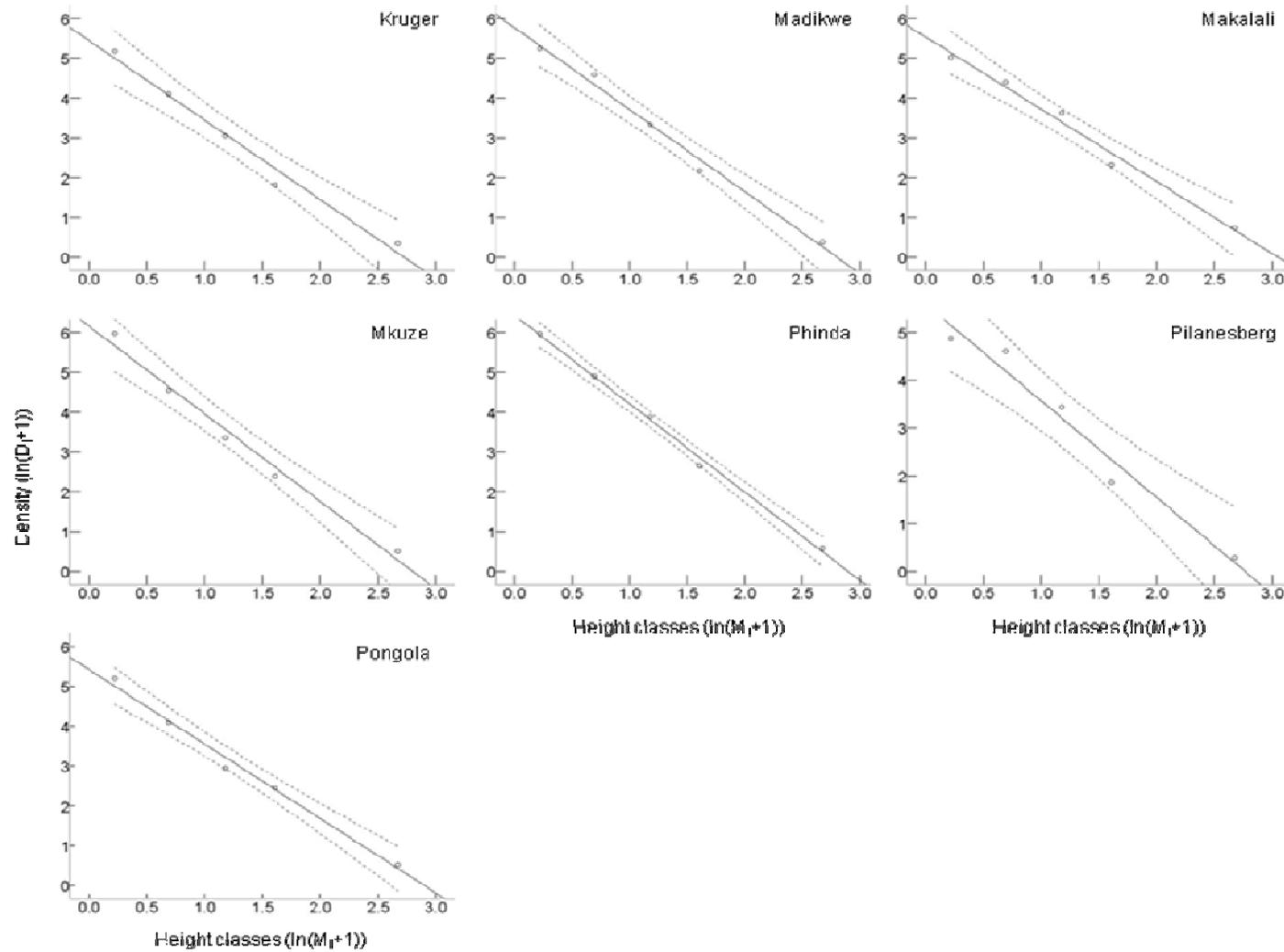
Factor	Seedling	Sapling	Small tree	Medium tree	Large tree
Time since introduction	-0.193**	0.024	0.067	-0.173**	-0.182**
Elephant density	-0.196**	-0.081	-0.044	0.026	0.003
Fire return period	0.225**	0.033	0.048	0.224**	0.298**
Rainfall	0.352**	0.151**	0.026	-0.041	-0.103*

Correlations were performed for each of five functional tree height classes including all species in seven protected areas in South Africa.

\*\* P < 0.01 ; \* P < 0.05



**Figure 3** Effects of time since elephant introduction, elephant density, fire return period and mean annual rainfall on tree densities for each height class across seven reserves (N = 565).



**Figure 4** Height class distributions of the woody vegetation in seven protected areas. The strong negative slopes, derived from linear regressions, indicate recruitment throughout all size classes ( $P \leq 0.003$ ,  $R^2 \geq 0.964$ ). The dotted lines indicate 95% confidence intervals.

**Table 3** The incidence of potential missing size classes per functional height class per reserve (incl. all transects), expressed as a percentage per species (between parentheses the number of species potentially present within the height class)<sup>1</sup>

Reserve	Missing height classes	Seedling ( $\leq 0.5$ m)	Sapling (0.51 – 1.5 m)	Small tree (1.5 – 3.0 m)	Medium tree (3.01 – 5 m)	Large tree ( $> 5.0$ m)
Kruger National Park central section	43.3 (31)	3.2 (31)	0 (31)	6.7 (30)	<b>34.5</b> (29)	42.3 (26)
Madikwe Game Reserve	18.2 (33)	0 (33)	0 (33)	3.0 (33)	9.1 (33)	16.7 (30)
Greater Makalali Private Game Reserve	33.3 (33)	3.0 (33)	0 (33)	9.1 (33)	12.5 (32)	29.6 (27)
Mkuze Game Reserve	43.9 (57)	1.8 (57)	0 (57)	8.8 (57)	24.6 (57)	38 (50)
Phinda Private Game Reserve	46.2 (65)	3.1 (65)	4.6 (65)	9.2 (65)	30.8 (65)	38.7 (62)
Pilanesberg National Park	32.4 (37)	0 (37)	0 (37)	0 (37)	19.4 (36)	33.3 (36)
Pongola Game Reserve	<b>51.7</b> (30)	<b>6.7</b> (30)	<b>6.7</b> (30)	<b>10.3</b> (29)	<b>34.5</b> (29)	<b>46.2</b> (26)

<sup>1</sup> Values in bold indicate the highest percentage per class

The incidence of missing classes was lowest in Madikwe for all but one height class (i.e. within the small tree class; Table 3), while the incidence was highest for all height classes in Pongola (but Kruger and Pongola share high incidence for medium tree class; Table 3).

No seedlings were absent in Madikwe and Pilanesberg. The more abundant species were all represented by individuals in the sapling class, with the exception of species in Phinda and Pongola, though incidences of missing species in this height class were low. Within each reserve, medium and large trees ( $\geq 5.0$  m) were most often absent of all size classes (Table 3).

### Effects at the species scale

Twelve species occurred in all seven protected areas. All twelve species were present within the seedling and sapling classes in Mkuze and Pilanesberg, within the sapling class in Madikwe and in the small tree class in Kruger, but these reserves had species missing in other size classes. In Makalali, Phinda and Pongola one or more of these twelve species were absent from all size classes. Also the twelve species occurred least often in the large tree class ( $\geq 5.0$  m), except in Phinda (Table 4).

Significant backward regression models were found for each height class including the twelve species (Table 5, see Appendix S2.2 for all significant full models per species). Seedling and sapling densities were affected by rainfall (positively), fire return period (positively) and elephant densities (seedlings: positively; saplings: negatively), while sapling densities were also positively impacted by time since elephant introduction. The densities of trees  $> 3$  m (i.e. medium and large trees) appear less susceptible to all four variables. Rainfall and fire return period positively affected densities within each height class. Elephant densities did not affect densities of trees taller than 3 m, but did affect seedling (positively), sapling (negatively) and small tree densities (mainly negatively). Time since elephant introduction did not affect seedlings and large trees ( $> 5$  m), but affected densities of saplings (positively), small trees (mainly positively) and medium trees (positively).

Some species showed a significant response to only one of the tested drivers of savanna dynamics (Appendix S2.2). *Combretum apiculatum* and *Grewia monticola* only showed a positive response to a prolonged fire return period, whereas *Acacia nilotica* and *Euclea natalensis* were only affected (positively) by rainfall. *Peltophorum africanum* responded only to elephant (i.e. negatively to elephant density and positively to time since elephant introduction).

**Table 4** The incidence of missing height classes per functional height class and reserve for the twelve species occurring in all seven reserves (% of the twelve species)<sup>1</sup>

Reserve	Seedling	Sapling	Small tree	Medium tree	Large tree
	(≤ 0.5 m)	(0.51 – 1.5 m)	(1.5 – 3.0 m)	(3.01 – 5 m)	(> 5.0 m)
					n = 11 species <sup>2</sup>
Kruger National Park central section	25.0	8.3	0	25.0	<b>41.7</b>
Madikwe Game Reserve	16.7	0	8.3	25.0	25.0
Greater Makalali Private Game Reserve	16.7	8.3	8.3	<b>33.3</b>	33.3
Mkuze Game Reserve	0	0	<b>16.7</b>	8.3	33.3
Phinda Private Game Reserve	8.3	8.3	8.3	16.7	8.3
Pilanesberg National Park	0	0	8.3	8.3	25.0
Pongola Game Reserve	<b>33.3</b>	<b>25.0</b>	<b>16.7</b>	<b>33.3</b>	33.3

<sup>1</sup> Values in bold indicate the highest percentage(s) within each functional height class.

<sup>2</sup> *Gymnosporia senegalensis* does not grow beyond 5 m (Coates Palgrave 2002)

**Table 5** Effect of savanna drivers on different tree height classes expressed as the percentage of species affected by these drivers within the seven reserves (n = 12 species present in all seven reserves; n = 11 for large trees)

Scale	Driver	<i>Size class</i>				
		Seedling (≤ 0.5 m)	Sapling (0.51 – 1.5 m)	Small tree (1.5 – 3.0 m)	Medium tree (3.01 – 5 m)	Large tree (> 5.0 m)
Local	Time since elephant introduction	0	17	25	8	0
Local	Elephant density	17	8	42	0	0
Local	Fire return period	33	17	25	8	18
Regional	Rainfall	42	8	8	8	18

Conversely *Grewia bicolor* was affected by rainfall (positively), fire (positively) and elephant (densities: negatively; time since introduction: positively; Appendix S2.2). No significant models were found for *Pappea capensis* or *Ziziphus mucronata*.

## DISCUSSION

The broad-scale distribution of woody cover in savanna landscapes has been well studied, however this is less so for woody densities, particularly within tree height classes. We show that the overall woody density among protected areas is variable, and that tree size classes are missing from the savanna landscape, indicating a disruption within the ‘natural’ tree size distribution. Rainfall, elephant and fire affected densities within these classes.

Our broad-scale analysis shows that woody density is variable among reserves, and is affected by both regional (i.e. rainfall) and local (i.e. elephant and fire) drivers. As expected, rainfall increased woody density, and is in particular an important driver for recruitment (i.e. seedlings and saplings) (cf. Higgins *et al.*, 2000; Kraaij & Ward, 2006). The time elapsed since elephant introduction appeared more detrimental to woody densities than did elephant density per se. A longer time since elephant introduction negatively affected medium and large trees, size classes generally destructively impacted by elephant through tree pushing and ring barking (Owen-Smith, 1988; Kerley *et al.*, 2008). Seedlings were also negatively affected, not only by time since introduction, but also by elephant density. The explanation for this is not clear. The negative effect of elephant on medium and large trees may in time inhibit recruitment as reproductive trees are being reduced by elephant. In addition, elephant introductions often occurred concurrent with the (re)introduction of other herbivore species, and generally numbers of all browsing herbivores have increased over time in these protected areas (R. Slotow, pers. obs.). Herbivores such as impala and nyala often impact on seedlings (Moe *et al.*, 2009; Lagendijk *et al.*, 2011), and could therefore confound any elephant effect. A longer fire return period increased woody density as it provides a window of opportunity for seedling establishment and survival, as well as an escape for woody individuals from the fire trap. Trees below 3 m in height can be retained within the fire trap during regimes of short fire return periods (Bond *et al.*, 2001; Bond & Archibald, 2003; Levick *et al.*, 2009). We found a positive effect on seedlings, medium and large trees with a prolonged fire return period. We therefore concur with Vanak *et al.* (2011) that fire can also cause mortality in large trees. However, the above needs to be interpreted with caution due to possible pseudoreplication. Additional studies are recommended to increase the external validity.

Tree height classes were indeed absent from the savanna landscape. At least 30% of the species in each reserve (with the exception of Madikwe: 18.2%) missed individuals within certain height strata. Individuals were most frequently absent from the medium and large tree classes (> 3 m) across all reserves, consistent with the size classes affected by elephant introduction time and fire return period in our regional scale analyses. Detailed fine scale investigation for these effects at the local scale is required.

Disruptions in tree size distributions appear to be mortality related. It seems recruitment is taking place, but the transition of trees into taller size classes is impacted by fire and elephant. The concern whether this is detrimental to population dynamics, and thus the persistence of species, requires further attention. However, it may be speculated that this is of more importance for trees than for shrubs. Parent trees which produce offspring are more often taller trees, while shrubs are usually shorter and within the fire and browsing trap when reproducing. This will be one of our future research endeavours.

Fire and herbivores (*e.g.* elephant) are important drivers of savanna dynamics which, as opposed to rainfall, can be actively managed by reserve management (Bond & Archibald, 2003; Van Wilgen *et al.*, 2004; Slotow *et al.*, 2005). Woody species respond differently to disturbance factors such as elephant and fire, and we can therefore propose ‘indicator’ species to detect single driver effects (*i.e.* rainfall, fire or elephant), which may thus facilitate monitoring of savanna drivers at multiple scales (*e.g.* reserve and regional scale). The effect of rainfall can be detected by monitoring either *Acacia nilotica* or *Euclea natalensis* and the effect of fire by *Combretum apiculatum* or *Grewia monticola*. Both *C. apiculatum* and *G. monticola* are slow growers and thus remain longer within the fire trap than fast growing species such as *Z. mucronata* or *S. birrea* (Van Wyk, 1984 in Zambatis, 2005). Although elephant utilise all twelve species (Wiseman *et al.*, 2004, references in Zambatis, 2005, de Boer *et al.*, 2000), only *P. africanum* showed a response to elephant on the population structure. The recognition of species specific responses is crucial when conserving species of key importance, such as marula *S. birrea* (Shackleton, 2002). In addition, Young *et al.* (2011) recognised the need for more site specific and local research for managers at the reserve scale. The species specific effects identified here can be used to monitor the effects of management interventions aimed to regulate fire and elephant impact at the local reserve scale, while at the same time to monitor the effect of regional scale shifts.

We acknowledge that height classes are not independent from each other, as there is a natural transition from one class to the other. However we do believe that by analysing the data per separate height class we contributed to the basic understanding of which drivers affect densities in different height classes. We also stress that woody densities within savanna ecosystems are also affected by other (a)biotic drivers, such as nutrients, geology and other herbivore species (Scholes & Walker, 1993; Vanak *et al.*, 2011), as well as complex interactions amongst these drivers (Eckhardt *et al.*, 2000; Van Wilgen *et al.*, 2004; Vanak *et al.*, 2011). The variability of woody densities across size classes is also affected by the ecological history (e.g. Staver *et al.* 2011). Including only elephant, fire return period and rainfall, allowed us to focus on single driver effects on different height classes. In addition, there is a need for long-term monitoring programs. These can detect change and elucidate the processes driving savanna dynamics, and thus confirm or reject results inferred from static population data (Obiri *et al.*, 2002).

The validity of comparing population structures with an inverse J-shaped curve in savannas is debatable. A second peak in the curve would be expected for small trees as the observed browsing and fire trap would retain more trees below 3 m in height. Savanna tree populations may thus more typically be described by a bimodal frequency distribution, with relatively more individuals in the seedling and small tree class, than in the other classes. However, the height class distributions per reserve for all species combined, do not display a bimodal curve and only two reserves display the inverse J-shaped curve. Regardless, the distributions in all reserves clearly show the browse- and fire trap, with a relative drop in density of medium and large trees. The fitting of a typical curve describing savanna tree population structures requires more attention.

As bush encroachment is expanding at the global scale (Wigley *et al.*, 2010), we here found evidence that the densities in the smaller height classes (i.e. seedling, sapling and medium trees:  $\leq 3$  m) can increase with a prolonged fire return period as well as increased rainfall. Of these two, only fire return period can be actively managed. However, shorter fire return periods in turn affect the transition into taller height classes, and as such may jeopardise the recruitment of reproductive adult trees and thus local persistence of the species. In addition, a longer elephant exposure time negatively affects medium and large trees, thereby exacerbating the effect of fire. The contrasting effects of different drivers on specific height classes illustrate the need to monitor changes in vegetation at both the regional and reserve scale. This is necessary to be able to respond to the effects of drivers at the global/regional scale (e.g. shifting CO<sub>2</sub> levels and rainfall) and the local/reserve scale, in order to conserve biodiversity across multiple scales.

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## REFERENCES

- Barnes, M.E. (2001) Effects of large herbivores and fire on the regeneration of *Acacia erioloba* woodlands in Chobe National Park, Botswana. *African Journal of Ecology*, 39, 340-350.
- Bond, W.J. & Archibald, S. (2003) Confronting complexity: fire policy choices in South African savanna parks. *International Journal of Wildland Fire*, 12, 381-389.
- Bond, W.J. & Keeley, J.E. (2005) Fire as a global 'herbivore': the ecology and evolution of flammable ecosystems. *Trends in Ecology and Evolution*, 20, 387-394.
- Bond, W.J., Smythe, K.A. & Balfour, D.A. (2001) Acacia species turnover in space and time in an African savanna. *Journal of Biogeography*, 28, 117-128.
- Bond, W.J., Woodward, F.I. & Midgley, G.F. (2005) The global distribution of ecosystems in a world without fire. *New Phytologist*, 165, 525-538.
- Bucini, G. & Hanan, N.P. (2007) A continental-scale analysis of tree cover in African savannas. *Global Ecology and Biogeography*, 16, 593-605.
- Chapin, F.S., Zavaleta, E.S., Eviner, V.T., Naylor, R.L., Vitousek, P.M., Reynolds, H.L., Hooper, D.U., Lavorel, S., Sala, O.E., Hobbie, S.E., Mack, M.C. & Díaz, S. (2000) Consequences of changing biodiversity. *Nature*, 405, 234-242.
- Coates Palgrave, K. (2002) *Trees of Southern Africa*. Struik Publishers, Cape Town.
- Condit, R., Sukumar, R., Hubbell, S.P. & Foster, R.B. (1998) Predicting population trends from size distributions: a direct test in a tropical tree community. *The American Naturalist*, 152, 495-509.

- de Boer, W.F., Ntumi, C.P., Correia, A.U. & Mafuca, J.M. (2000) Diet and distribution of elephant in the Maputo Elephant Reserve, Mozambique. *African Journal of Ecology*, 38, 188-201.
- Delsink, A.K. (2006) *The costs and consequences of immunocontraception implementation in elephants at Makalali Conservancy, South Africa*. University of KwaZulu-Natal, Durban.
- Druce, D. (2000) *Factors affecting millipede, centipede and scorpion diversity in a savanna environment*. University of KwaZulu-Natal, Durban.
- Druce, H.C., Pretorius, K. & Slotow, R. (2008) The response of an elephant population to conservation area expansion: Phinda Private Game Reserve, South Africa. *Biological Conservation*, 141, 3127-3138.
- Du Toit, J.T. (2003) Large herbivores and savanna heterogeneity. *The Kruger Experience: Ecology and management of savanna heterogeneity* (ed. by J.T. Du Toit, K.H. Rogers and H.C. Biggs), pp. 292-309. Island Press, Washington.
- Du Toit, J.T. & Cumming, D.H.M. (1999) Functional significance of ungulate diversity in African savannas and the ecological implications of the spread of pastoralism. *Biodiversity and Conservation*, 8, 1643-1661.
- Eckhardt, H.C., van Wilgen, B.W. & Biggs, H.C. (2000) Trends in woody vegetation cover in the Kruger National Park, South Africa, between 1940 and 1998. *African Journal of Ecology*, 38, 108-115.
- Higgins, S.I., Bond, W.J. & Trollope, W.S.W. (2000) Fire, resprouting and variability: a recipe for grass-tree coexistence in savanna. *Journal of Ecology*, 88, 213-229.
- Kalwij, J.M., de Boer, W.F., Mucina, L., Prins, H.H.T., Skarpe, C. & Winterbach, C. (2010) Tree cover and biomass increase in a southern African savanna despite growing elephant population. *Ecological Applications*, 20, 222-233.
- Kerley, G.I.H., Landman, M., Kruger, L., Owen-Smith, N., Balfour, D., de Boer, W.F., Gaylard, A., Lindsay, K. & Slotow, R. (2008) Effects of elephants on ecosystems and biodiversity. *Elephant Management: A Scientific Assessment for South Africa* (ed. by R.J. Scholes, Mennell, K.G.), pp. 146-205. Witwatersrand University Press, Johannesburg.
- Kettles, R. & Slotow, R. (2009) Management of free-ranging lions on an enclosed game reserve. *South African Journal of Wildlife Research*, 39, 23-33.
- Kraaij, T. & Ward, D. (2006) Effects of rain, nitrogen, fire and grazing on tree recruitment and early survival in bush-encroached savanna, South Africa. *Plant Ecology*, 186, 235-246.

- Legendijk, D.D.G., Mackey, R.L., Page, B. & Slotow, R. (2011) The effects of herbivory by a mega- and mesoherbivore on tree recruitment in Sand Forest, South Africa. *PLoS ONE*, 6, e17983.
- Levick, S., Asner, G.P., Kennedy-Bowdoin, T. & Knapp, D.E. (2009) The relative influence of fire and herbivory on savanna three-dimensional vegetation structure. *Biological Conservation*, 142, 1693-1700.
- Lykke, A.M. (1998) Assessment of species composition change in savanna vegetation by means of woody plants' size class distributions and local information. *Biodiversity and Conservation*, 7, 1261-1275.
- Macandza, V.A., Owen-Smith, N. & Cross, P.C. (2004) Forage selection by African buffalo in the late dry season in two landscapes. *South African Journal of Wildlife Research*, 34, 113-121.
- Mackey, R.L., Page, B.R., Duffy, K.J. & Slotow, R. (2006) Modelling elephant population growth in small, fenced, South African reserves. *South African Journal of Wildlife Research*, 36, 33-43.
- Moe, S.R., Rutina, L.P., Hytteborn, H. & Du Toit, J.T. (2009) What controls woodland regeneration after elephants have killed the big trees? *Journal of applied ecology*, 46, 223-230.
- Moolman, L. (2007) *Elephant browsing patterns in the Pilanesberg National Park*. University of KwaZulu-Natal, Durban.
- Morgan, S., Mackey, R.L. & Slotow, R. (2009) A priori valuation of land use for the conservation of black rhinoceros (*Diceros bicornis*). *Biological Conservation*, 142, 384-393.
- Mulqueeny, C.M., Goodman, P.S. & O'Connor, T.G. (2010) Landscape-level differences in fire regime between block and patch-mosaic burning strategies in Mkuzi Game Reserve, South Africa. *African Journal of Range and Forage Science*, 27, 143-150.
- Obiri, J.A.F., Lawes, M.J. & Mukolwe, M. (2002) The dynamics and sustainable use of high-value tree species of the coastal Pondoland forests of the Eastern Cape Province, South Africa. *Forest Ecology and Management*, 166, 131-148.
- Owen-Smith, R.N. (1988) *Megaherbivores: the influence of very large body size on ecology*. Cambridge University Press, Cambridge.
- Sankaran, M., Hanan, N.P., Scholes, R.J., Ratnam, J., Augustine, D.J., Cade, B.S., Gignoux, J., Higgins, S.I., Le Roux, X., Ludwig, F., Ardo, J., Banyikwa, F., Bronn, A., Bucini, G., Caylor, K.K., Coughenour, M.B., Diouf, A., Ekaya, W., Feral, C.J., February, E.C., Frost, P.G.H., Hiernaux, P., Hrabar, H., Metzger, K.L., Prins, H.H.T., Ringrose, S., Sea, W.,

- Tews, J., Worden, J. & Zambatis, N. (2005) Determinants of woody cover in African savannas. *Nature*, 438, 846-849.
- Scholes, R.J. & Walker, B.H. (1993) *An African savanna: synthesis of the Nylsvlei study*. Cambridge University Press.
- Shackleton, C. (2002) Growth and fruit production of *Sclerocarya birrea* in the South African lowveld. *Agroforestry Systems*, 55, 175-180.
- Shannon, G., Page, B., Slotow, R. & Duffy, K. (2006) African elephant home range and habitat selection in Pongola Game Reserve, South Africa. *African Zoology*, 41, 37-44.
- Shannon, G., Druce, D.J., Page, B.R., Eckhardt, H.C., Grant, R. & Slotow, R. (2008) The utilization of large savanna trees by elephant in southern Kruger National Park. *Journal of Tropical Ecology*, 24, 281-289.
- Skarpe, C. (1992) Dynamics of savanna ecosystems. *Journal of Vegetation Science*, 3, 293-300.
- Slotow, R. & Van Dyk, G. (2001) Role of delinquent young "orphan" male elephants in high mortality of white rhinoceros in Pilanesberg National Park, South Africa. *Koedoe*, 44, 85-94.
- Slotow, R., Garaï, M.E., Reilly, B., Page, B. & Carr, R.D. (2005) Population dynamics of elephants re-introduced to small fenced reserves in South Africa. *South African Journal of Wildlife Research*, 35, 23-32.
- Staver, A.C., Bond, W.J., Stock, W.D., Jansen van Rensburg, S. & Waldram, M.S. (2009) Browsing and fire interact to suppress tree density in an African savanna. *Ecological Applications*, 19, 1909-1919.
- Staver, A.C., Bond, W.J., February, E.C. (2011) History matters: tree establishment variability and species turnover in an African savanna. *Ecosphere*, 2, art49. doi: 10.1890/ES11-00029.1
- Trinkel, M., Funston, P., Hofmeyr, M., Hofmeyr, D., Dell, S., Packer, C. & Slotow, R. (2010) Inbreeding and density-dependent population growth in a small, isolated lion population. *Animal Conservation*, 13, 374-382.
- Van de Koppel, J. & Prins, H.H.T. (1998) The importance of herbivore interactions for the dynamics of African savanna woodlands; an hypothesis. *Journal of Tropical Ecology*, 14, 565-576.
- Van Wilgen, B.W., Biggs, H.C., O'Regan, S.P. & Marè, N. (2000) A fire history of the savanna ecosystems in the Kruger National Park, South Africa, between 1941 and 1996. *South African Journal of Science*, 96, 167-178.

- Van Wilgen, B.W., Govender, N., Biggs, H.C., Ntsala, D. & Funda, X.N. (2004) Response of savanna fire regimes to changing fire-management policies in a large African National Park. *Conservation Biology*, 18, 1533-1540.
- Vanak, A.T., Shannon, G., Thaker, M., Page, B., Grant, R. & Slotow, R. (2011) Biocomplexity in large tree mortality: interaction between elephant, fire and landscape in an African savanna. *Ecography*: doi: 10.1111/j.1600-0587.2011.07213.x
- Walker, B.H., Stone, L., Henderson, L. & Vernelde, M. (1986) Size structure analysis of the dominant trees in a South African savanna. *South African Journal of Botany*, 52, 397-402.
- Wigley, B.J., Bond, W.J. & Hoffman, M.T. (2010) Thicket expansion in a South African savanna under divergent land use: local vs. global drivers? *Global Change Biology*, 16, 964-976.
- Wilson, B.G. & Witkowski, E.T.F. (2003) Seed banks, bark thickness and change in age and size structure (1978-1999) of the African savanna tree, *Burkea africana*. *Plant Ecology*, 167, 151-162.
- Wiseman, R., Page, B.R. & O'Connor, T.G. (2004) Woody vegetation change in response to browsing in Ithala Game Reserve, South Africa. *South African Journal of Wildlife Research*, 34, 25-37.
- Young, K.D. & Van Aarde, R.J. (2011) Science and elephant management decisions in South Africa. *Biological Conservation*, 144, 876-885.
- Zambatis, G. (2005) Plants utilised by elephants. *Elephants Effects on Biodiversity: an executive summary assessing the knowledge and understanding informing elephant management in SANParks. Scientific Report* (ed. by C.C. Grant), pp. 191-210.

### CHAPTER 3

#### **Woody Vegetation Communities and Herbivory in a South African Savanna: Effects of Landscape Position and Elephant**

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**Abstract**

The effect of landscape position on vegetation and herbivory is well documented for grasslands and grazers, but less so for trees and browsers. We examined the effect of hillslope position on tree species assemblages, resource availability (i.e., structural diversity and tree densities), and browsing pressure, separating this from the response to short-term elephant presence. We therefore sampled vegetation quadrats on footslopes and crests in areas with and without elephant access. Woody species assemblages were similar between areas with and without elephant but differed between slope positions, with higher species richness on footslopes. Variation in species assemblages was best explained by ECEC, Zinc, sand and clay. Slope position affected tree population structures, but not height distributions, nor tree or stem densities. Elephant access affected tree population structure and height distribution, with greater sapling densities in elephant access areas. Elephant access did not affect overall tree or stem densities. Elephant and mesoherbivore browsing pressures were unaffected by slope position, but mesoherbivore browsing pressure was lower with higher elephant browsing pressure on crests. Indirectly, elephant seem to facilitate the survival of saplings, via displacement of mesoherbivores, and thus regeneration of saplings into taller height classes. The absence of a direct (short-term) elephant browsing effect on vegetation assemblages and overall densities is particularly relevant for elephant management, as there is a bias towards only reporting negative effects in the literature. The effects of slope position found here are in contrast with other studies, and illustrate the importance of acknowledging the complexity in local topography.

**Key words:** browsing pressure; catena; displacement; facilitation; mesoherbivores; population structure; sapling; spatial heterogeneity;

## Introduction

The African savanna biome, characterised by a high degree of spatial heterogeneity, harbours one of the most diverse assemblages of large herbivores (Du Toit and Cumming 1999; Du Toit 2003). As would be expected, species will use the landscape differently depending on their specific nutritional requirements and the spatial heterogeneity of the available resources (Seagle and McNaughton 1992; Prins and Van Langevelde 2008). Many complex factors determine herbivore foraging behaviour and the consequent use of the landscape, including the quality, availability and spatial distribution of resources (Wronski 2002), as well as predation risk and competition from other herbivores (Prins and Iason 1989; Thaker et al. 2011). Therefore, the impact of herbivores on vegetation is spatially heterogeneous across the savanna landscape (Seagle and McNaughton 1992; Nellemann et al. 2002; Kerley et al. 2008).

Studies that examine the spatial components of foraging impacts in the savanna ecosystem often focus on the distance to water sources at the landscape level (Smit et al. 2007; Kalwij et al. 2010). This paper focuses on the smaller spatial scale of hillslopes. Although the effect of slope position (e.g., footslopes vs. crests) on the foraging behaviour of grazers has been well studied (Macandza et al. 2004; Grant and Scholes 2006), less is known for browsers. In Botswana, areas with gentle undulating slopes were found to have a higher browsing pressure by African elephant *Loxodonta africana* than flat areas (Nellemann et al. 2002). From the plant perspective, steep slopes and crests can serve as spatial refugia from herbivory, as seen for charismatic species such as Baobab *Adansonia digitata*, Marula *Sclerocarya birrea* and *Euphorbia* spp. (Weyerhaeuser 1985; Edkins et al. 2007; Kerley et al. 2008; Cowling et al. 2009).

Woody vegetation communities and degree of herbivory are expected to differ along the slope gradient, mainly because of the variation in ecohydrological conditions on the hillslope (Ludwig et al. 2005). During the wet season, water and sediments are transported downslope through runoff, where they are captured by the vegetation in lower areas (run-on) and partially stored in the soil (Ludwig et al. 2005; Jacobs et al. 2007). Nutrients accumulate at lower slope positions, which results in a high quality soil resource base for plant regeneration and growth (Ludwig et al. 2005; Jacobs et al. 2007). Consequently, plants at lower slope positions should be of a higher nutritional quality and more palatable than their upslope counterparts (Grant and Scholes 2006), and we therefore expect that lower slope vegetation will be preferred by herbivores. In addition, runoff prolongs the growing seasons in low-lying areas, resulting in a different plant species composition along the slope gradient (Illius and O'Connor 2000).

Vegetation dynamics and composition are also strongly influenced by herbivore impacts. Elephant impact is a strong determinant of savanna dynamics and is a major concern in the savanna system (Owen-Smith 1988; Kerley et al. 2008). Most typically, the foraging behaviour of elephant, which includes bark removal and toppling of trees, can negatively affect tree populations (Owen-Smith 1988; Prins and Van der Jeugd 1993; Kerley et al. 2008). While Belsky (1984) and Prins and Van der Jeugd (1993) have indicated that mesoherbivores (medium-size herbivores between 50 - 450 kg; Fritz et al. 2002; de Garine-Wichatitsky et al. 2004) can negatively affect regeneration of woody vegetation, only more recently have research efforts again started to include the impact of mesoherbivores, illustrated by the work of Moe et al. (2010) on impala *Aepyceros melampus* in riparian woodlands and Lagendijk et al. (2011a,b) on nyala *Tragelaphus angasii* in Sand Forest. Elephant and mesoherbivores can interact in their foraging impacts, as elephant facilitate foraging for mesoherbivores by increasing browse availability at lower levels after impacting large trees (Rutina et al. 2005; Makhabu et al. 2006). On the other hand, interference competition occurs between elephant and other herbivores at waterholes (Valeix et al. 2007), and elephant are known to displace meso- and smaller-sized herbivores in Sand Forest (Lagendijk et al. 2011b). Whether competition or facilitation between elephant and mesoherbivores affect their impact on vegetation at the hillslope scale is unknown.

In this study, we examined woody vegetation communities at the hillslope scale, and the effect and interaction of herbivory by elephant and mesoherbivores to understand differences in vegetation composition and structure. We also examined the effect of soil properties on species assemblages on footslopes and crests. Specifically, we tested whether (1) footslopes differ from crests, and whether (2) short-term access of elephant affects tree species assemblages, resource availability (i.e., tree densities and structural diversity), and browsing pressure. We also examined whether (3) browsing intensity by elephant affects herbivory by mesoherbivores. We expect tree species assemblages to differ between slope positions, in response to higher soil nutrient and browsing levels at the footslopes. Due to expected higher nutrient and moisture levels, we also expect a higher tree density on footslopes with a concomitant higher browsing pressure compared to crests, resulting in dissimilar height class distributions of the woody species. We further expect a facilitating effect of elephant browsing on herbivory by mesoherbivores, by making more browse available at lower height levels.

## Methods

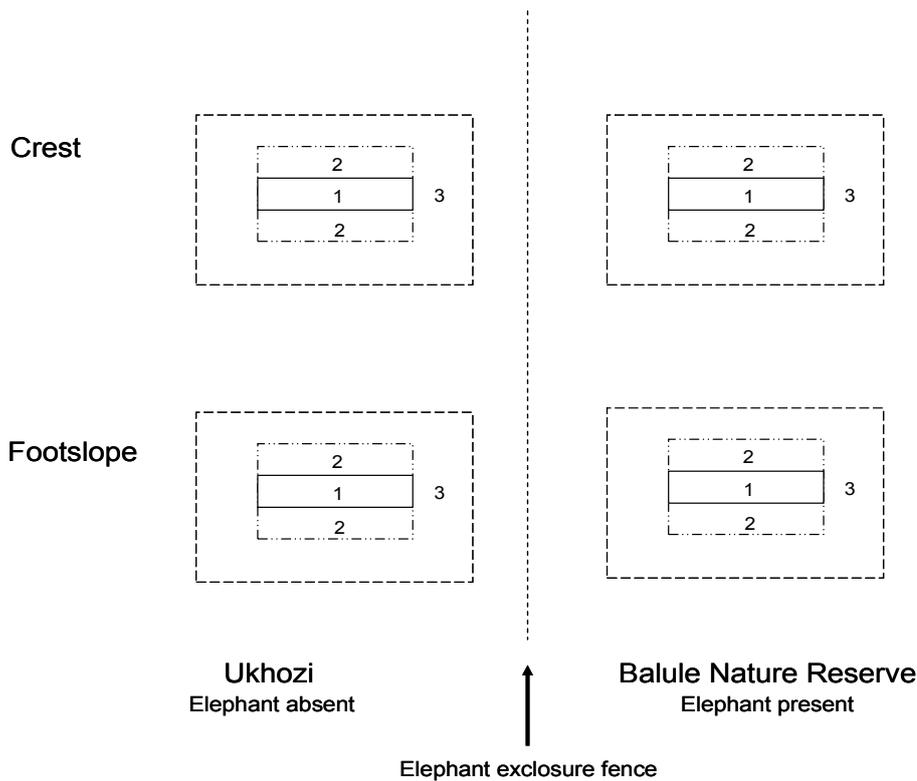
### *Study area*

We conducted this study in Balule Nature Reserve (hereafter Balule; 350 km<sup>2</sup>) which borders Kruger National Park in Limpopo Province, South Africa (24°21' - 24°17' S; 31°01' - 30°95' E). The open savanna woodland is dominated by *Combretum apiculatum*, *Grewia* spp., *Acacia nigrescens* and *Sclerocarya birrea*. Balule has a moderate undulating topography with elevations ranging from 340 - 425 m above sea level. The underlying substrate is granite with soapstone outcrops, nutrient poor shallow orthic soils with quartz gravel higher up the slopes, and rich red soils in the lower lying areas (Ferguson 1997; M. Cesare, pers. comm.). The climate is sub-tropical with hot, wet summers (November-April) and cool, dry winters (May-October). Temperatures range from 4 - 40°C, with a mean annual rainfall of 401 mm (1985-2007). Rainfall has been variable since 2005, with a wet year in 2006, and dry years in 2005 and 2007 (Peel 2007).

Fences between Balule and neighbouring reserves were removed in 2005, after which elephants moved into Balule. Before 2005, only seven elephants were present in Balule (M. Cesare, pers. comm.), and the effect of such a low elephant density would presumably have been minimal, especially since elephants were locally extinct until 1903 (Whyte et al. 1999). Part of this study was conducted within Ukhozi Nature Reserve (hereafter Ukhozi; 20 km<sup>2</sup>), which is part of Balule. Between 1987 and 2007, Ukhozi was partially used as a breeding farm for African buffalo *Syncerus caffer*, for which 15 km<sup>2</sup> were fenced off (C. Ferguson, pers. comm.). The Balule areas bordering Ukhozi were, at that time, used as private and tourist game viewing areas. In November 2007 fences were replaced with an electric elephant exclusion fence, allowing all wildlife, except giraffe *Giraffa camelopardalis* and elephant, to move freely between Balule and Ukhozi. Giraffe density in Ukhozi was 0.3 km<sup>-2</sup> (Balule 0.78 km<sup>-2</sup>) and elephant density in Balule was 1.17 km<sup>-2</sup>. Other browsing ungulates in Ukhozi include kudu *Tragelaphus strepsiceros* (0.35 km<sup>-2</sup>; Balule 1.45 km<sup>-2</sup>), impala (10 km<sup>-2</sup>; Balule 13.03 km<sup>-2</sup>) and bushbuck *Tragelaphus scriptus* (0.25 km<sup>-2</sup>; Balule no count available). Densities were derived from helicopter game counts in 2007.

### *Experimental design*

Five north-facing hillslope sites were selected along the border of Ukhozi (i.e., the 15 km<sup>2</sup> elephant free zone) and Balule. Distances between sites ranged from 0.8 to 6.0 km. Each of the five sites consisted of four plots (Fig. 1); two on each reserve (elephant effect: elephant presence vs. absence), and each of these two positioned on either the crest or footslope of the hill (slope



**Figure 1** Schematic overview of the four treatments (slope position: footslope vs. crest; elephant: absent vs. present) as laid out on each of the five sites. Vegetation within each treatment was recorded using three quadrats: (1) seedlings only:  $\leq 0.5$  m; (2) woody individuals above 0.5 m; (3) species not encountered in either quadrat 1 or 2 (all height classes included).

position effect). Bottomlands, where the largest effect is expected, were too narrow in size to sample, and we therefore selected the footslope. Our design resulted in four treatments: (1) crest without elephant; (2) crest with elephant (3); footslope without elephant; (4) footslope with elephant ( $N = 5$  for each treatment). Elephants are known to walk up to the Ukhozi fence, and therefore any potential fence (edge) effects due to plot placement are unlikely.

#### *Woody vegetation sampling*

The woody vegetation was sampled in December 2008. Three quadrats were placed in each plot (Fig. 1). Quadrat 1 (2 x 40 m) where only seedlings ( $\geq 0.02$  m and  $\leq 0.5$  m) were recorded was nested within quadrat 2 (30 x 40 m) where individuals  $> 0.5$  m were recorded, was nested within quadrat 3 (50 x 100 m) where individuals of additional species, i.e., species not encountered in either quadrat (1) or (2) were recorded, including all height classes. This sampling design is similar to Kalwij et al. (2010). In each quadrat, all woody individuals were counted, identified to species and we recorded diameters above the buttress swelling (stems  $\geq 0.1$  cm) and tree height.

Diameters and the heights of trees to 2 m were also measured, and the heights of trees  $\geq 2$  m were estimated using the height of an observer as a scale following Shannon et al. (2008).

#### *Soil properties*

Soil samples in relation to slope position were collected in May 2010. A composite soil sample of 500 g (consisting of 10 random samples lumped per plot) was taken from the top 10 cm of the soil layer (cf. Holdo and McDowell 2004). Litter and stones larger than 1 cm in diameter were removed upon sampling. Samples were air dried prior to transportation. The following properties were analysed from the soil samples at the Soil Fertility and Analytical Service Section of the Agricultural Research Council (ARC) in Cedara, South Africa: P, K, Total N, Cu, Ca, Mg, Mn, Zn, pH, effective cation exchange capacity (ECEC) and texture (% silt, sand and clay), following Boyes et al. (2010).

#### *Browsing pressure*

Browsing events on trees by mesoherbivores (i.e., impala or bushbuck) and elephant were recorded. Leaf stripping and branch removal by even young elephant is easily detected, as well as single bites by mesoherbivores. In order to identify which herbivore species had utilised the tree, we identified the part of the plant used, height of the removal, amount of biomass removed, and the sharpness of the bite (ungulate) or break (elephant). Only browsing events positively ascribed to either elephant or mesoherbivores were included in the analyses.

#### *Data-analyses*

##### *Differences in woody vegetation*

Woody densities were expressed per 1 ha for comparison. We analysed species richness (total number of species) and tree species assemblages (which includes both composition and abundance of species) in order to determine if vegetation communities differed between footslopes and crests, and with or without elephant (Ukhozi vs. Balule; representing elephant absence vs. presence respectively). Differences in species richness were tested using a nested ANOVA design, in which slope position was nested in site and elephant presence nested in slope position. A two-way crossed analysis of similarity (ANOSIM, using PRIMER) was used to test for differences in species assemblages between slope position and elephant effect (Clarke and Warwick 2001). Species abundances were fourth-root transformed, which reduces the influence of the more abundant species in the calculation of the Bray-Curtis dissimilarities (Clarke and Warwick 2001). ANOSIM calculates the R statistic which ranges between 0 - 1; the closer a

significant R value is to one, the more distinct the species assemblages (Clarke and Warwick 2001).

Two possible demographic responses to browsing can be expected, namely increased mortality or a coppicing response. Therefore, we investigated changes in both the density of individuals (which measures mortality, but also reflects recruitment), and stem density (which measures the coppicing response and the mortality of stems). Nested ANOVA (slope position nested in site, elephant presence nested in slope position) were used to test if footslopes have higher densities of trees and stems, and whether this was affected by elephant presence.

To prevent species characteristics obscuring the analyses of the structural distributions of trees (both in height and diameter) and browsing pressure, the following analyses were restricted only to woody species occurring in all four treatments. *Grewia* spp. and *Ozoroa* spp. were pooled within genus due to hybridisation within each genus in the study area. Consequently 19 species (i.e., totalling to 97 % of all individual trees) were included in the analyses (Appendix S3.1). Trees were allocated to five height classes (0.2 - 0.5 m: seedling; 0.51 -1.5 m: sapling; 1.51 – 3 m: small tree; 3.1 – 5 m: medium tree; > 5.1 m: tall tree (Augustine and McNaughton 2004; Babweteera et al. 2007; Shannon et al. 2008; Kalwij et al. 2010). These height classes roughly correspond to the escape heights of impacts from different-size browsing herbivores in savannas.

The effects of slope position, elephant presence and site on the densities of each functional height class of the 19 tree species were analysed using a nested MANOVA. To satisfy assumptions of normality and equality of variances, we applied  $\log_{10}$ -transformations on saplings, small- and medium trees.

Tree populations are considered to be regenerating when the frequency distribution of tree diameters follows an inverse J-shape (Lykke 1998; Obiri et al. 2002). This translates to a high abundance of seedlings, which represents sufficient recruitment, and a low abundance of tall trees. A deviation from the ideal J-shape is indicative of disturbance (Walker et al. 1986). We used 18 different size classes with 1 cm intervals (to 7 cm diameter), thereafter 2 cm intervals (to 15 cm diameter), 5 cm intervals (to 30 cm diameter) and 10 cm intervals (to 60 cm). A G-test was used to determine whether diameter size distributions differed among the four treatments for each of the 19 species. To prevent Type I errors from running four pair-wise G-tests, a Bonferroni-adjusted alpha of 0.0125 was used.

*Differences in soil properties*

A nested MANOVA was used to test if soils had higher nutrient concentrations on footslopes than on crests (with slope position nested in site; elephant presence was not included as a factor because the short exposure to elephant would not be expected to influence soil properties). The soil properties P, K, Total N, Cu, Mg, Mn, Zn, pH, ECEC, silt and clay were included in the model after arcsine transformation (except for pH and ECEC). Soil parameters were tested for correlation using Spearman rank correlations and omitted when  $r_s \geq 0.95$  (Clarke and Warwick 2001). Ca was, therefore, omitted from the analyses due to high correlation with ECEC ( $r_s = 0.985$ ,  $P < 0.001$ ).

*Relationship between species assemblages and soil parameters*

The relationship between species assemblages and soil parameters was investigated using the BIO-ENV procedure in PRIMER (Clarke and Warwick 2001). All soil parameters were arcsine transformed with the exception of pH and ECEC. Ca was again omitted due to high correlation with ECEC. In order to match the species assemblage data to the soil parameters, a similarity matrix of the latter based on normalised Euclidean distance was used, which was linked to the species similarity matrix. During the BIO-ENV procedure, the parameters maximising the rank correlation ( $r_s$ ) between the two matrices are selected, and thus provide the best match for explaining the variation in species assemblages.

*Differences in browsing pressure*

To determine if browsing pressure was higher at footslopes than at crests, or affected by elephant access, we analysed browsing pressure by mesoherbivores using a nested ANOVA. Browsing pressure by mesoherbivores on the 19 species was assessed using absolute browsing pressure, which was calculated as the number of browsing events (e.g. impacted trees) per plot. Elephant browsing pressure on these species was calculated similarly, and, using ANOVA, we tested if elephant browsing pressure was higher at footslopes than at crests.

We used a linear regression to determine if elephant browsing affected herbivory by mesoherbivores. Elephant browsing was measured as absolute browsing events. To control for among-site effects (i.e., local non-elephant density), absolute browsing events by mesoherbivores in Balule (elephant present) were subtracted by their browsing events on Ukhozi (elephant absent) for each pair of corresponding plots, which gives us the relative browsing response by mesoherbivores to elephant browsing. Mesoherbivores could move freely across the fence.

All dependent variables were normally distributed, and otherwise transformed, to meet assumptions of normality and equality of variances, as mentioned above. ANOSIM and BIO-ENV were analysed in PRIMER 6 (PRIMER-E Ltd.). All other statistical tests were performed using SPSS 15.0 (SPSS Inc., Chicago, USA).

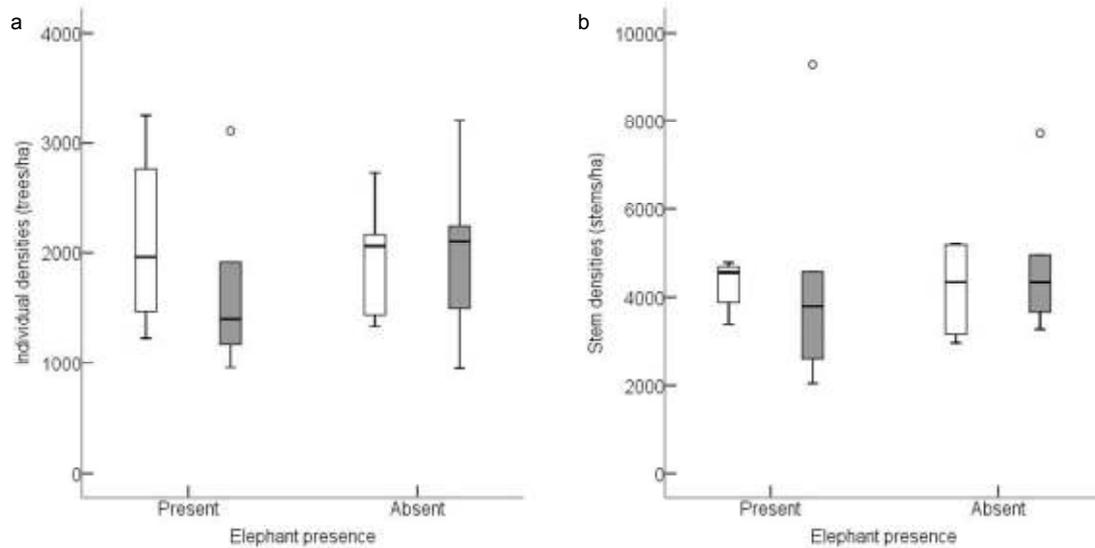
## Results

### *Differences in woody vegetation*

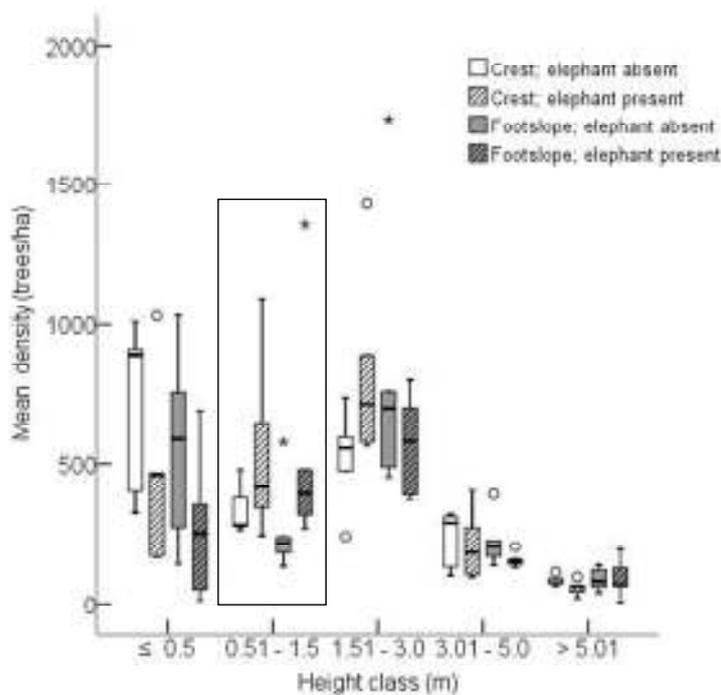
In total, 4660 individual trees of 68 woody species were recorded. Species richness was similar among the five sites ( $P = 0.34$ ) and between areas with and without elephant presence ( $P = 0.42$ ), but was higher on footslopes than on crests ( $F_{4,8} = 5.566$ ,  $P = 0.02$ ). Footslopes harboured 20 species not encountered on crests, and crests had 13 species that were not recorded on footslopes, consequently both slope positions had 35 species in common. Concordant with this, ANOSIM indicated that woody species assemblages on footslopes differed significantly from assemblages on crests (Bray-Curtis:  $R = 0.318$ ,  $P = 0.004$ ), but were similar in areas with and without elephant presence (ANOSIM:  $R = 0.004$ ,  $P = 0.48$ ), indicating no short-term effect of elephant presence on species assemblages.

Contrary to our expectation, overall tree densities (i.e., including all height classes and all species) were not significantly higher on footslopes ( $P = 0.21$ ), and were similar between elephant treatments ( $P = 0.68$ ; Fig. 2). Stem densities were also not significantly greater on footslopes ( $P = 0.10$ ), or higher with elephant access ( $P = 0.88$ ; Fig. 2). Given that tree and stem densities were not significantly different across elephant treatment and slope positions, there was no coppicing response. There was a significant site effect for stem densities ( $F_{4,8} = 6.451$ ,  $P = 0.01$ ), i.e., some sites had higher coppicing than others, but site did not significantly explain individual densities ( $P = 0.09$ ).

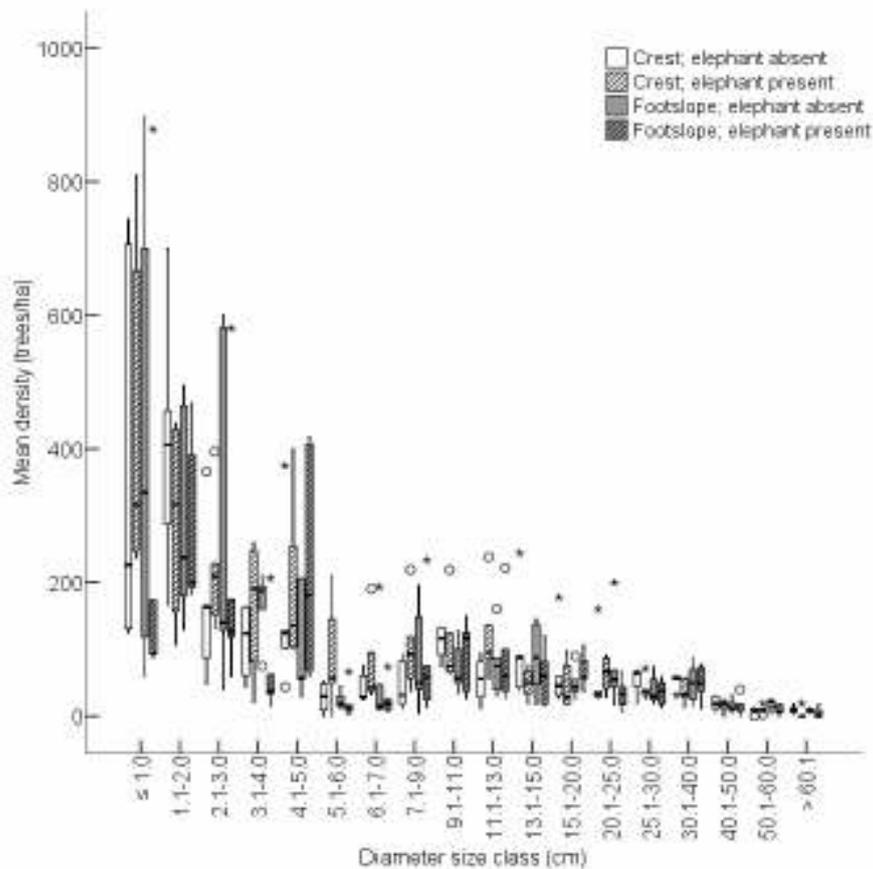
The MANOVA showed a significant effect of elephant presence (Pillai's trace:  $F_{10,10} = 3.363$ ,  $P = 0.03$ ; Fig. 3) on the densities of the different tree height classes (restricted to 19 species occurring in all four treatments). Subsequent ANOVAs indicated higher sapling (0.51 -1.5 m) densities in the presence of elephants ( $F_{2,8} = 2.416$ ,  $P = 0.02$ ), suggesting displacement of mesoherbivores by elephant (see below). Slope position and site did not affect densities of functional height classes (slope position: Pillai's trace:  $F_{20,28} = 1.325$ ,  $P = 0.24$ ; site: Pillai's trace:  $F_{20,28} = 1.602$ ,  $P = 0.12$ ).



**Figure 2** Densities of all woody species in areas with elephant presence and absence per slope position (crests: white bars; footslopes: grey bars): (a) individual densities (trees/ha); (b) stem densities (stems/ha, which includes coppicing effects). Shown are range (whiskers), 25 and 75 % quartiles (box), median (line) and circles are outlying values. N = 5 replicates per treatment.



**Figure 3** Mean density of trees across the height classes for the 19 species combined per treatment. Note the higher sapling densities in presence of elephant. Elephant presence and slope position had no significant effect on densities at any of the other height classes. Data are range (whiskers), 25 and 75 % quartiles (box), median (line), stars and circles are extreme and outlying values, respectively. N = 5 replicates per combination of slope position and elephant presence.



**Figure 4** Mean density of trees across diameter size classes for 19 species combined per treatment. Note the lower density on the footslope with elephant present in the  $\leq 1$  cm class. Data are range (whiskers), 25 and 75 % quartiles (box), median (line), stars and circles are extreme and outlying values respectively. N=5 replicates per combination of slope position and elephant presence.

Population structures of trees were assessed using the diameter distribution of all 19 species. Diameter size distributions were significantly different among treatments ( $G_5 = 3173.29$ ,  $P \leq 0.0125$  for all pair-wise comparisons; Fig. 4), indicating an effect of both slope position and elephant. Most noticeable, was the lower density within the  $\leq 1$  cm class on the footslope with elephant present. In general, population structures approached a bimodal distribution.

*Differences in soil properties and the relationship between species assemblages and soil properties*

Soil properties were significantly affected by slope position (Pillai's trace:  $F_{50,25} = 2.093$ ,  $P = 0.024$ ), but not by site ( $P = 0.17$ ). Footholds had significantly higher concentrations of P ( $F_{5,10} = 3.401$ ,  $P = 0.047$ ), K ( $F_{5,10} = 5.310$ ,  $P = 0.012$ ), Mg ( $F_{5,10} = 7.565$ ,  $P = 0.004$ ), and a higher effective cation exchange capacity (ECEC ~ to Ca:  $F_{5,10} = 8.684$ ,  $P = 0.002$ ), but crests had higher concentrations of Cu ( $F_{5,10} = 14.200$ ,  $P < 0.0001$ ). Slope position did not have a significant effect on concentrations of Mn ( $P = 0.087$ ), Zn ( $P = 0.734$ ), total N ( $P = 0.454$ ), pH ( $P = 0.070$ ), silt ( $P = 0.696$ ) and clay ( $P = 0.593$ ). Variation in woody species assemblages between slope positions was best explained by ECEC (ECEC ~ to Calcium), Zn, sand (%) and clay (%) (BIO-ENV:  $\rho_s = 0.374$ ). Species associated with high concentrations of these soil properties were species such as *Acacia senegal*, *Balanites maughamii*, *Manilkara mochisia* and *Pappea capensis*.

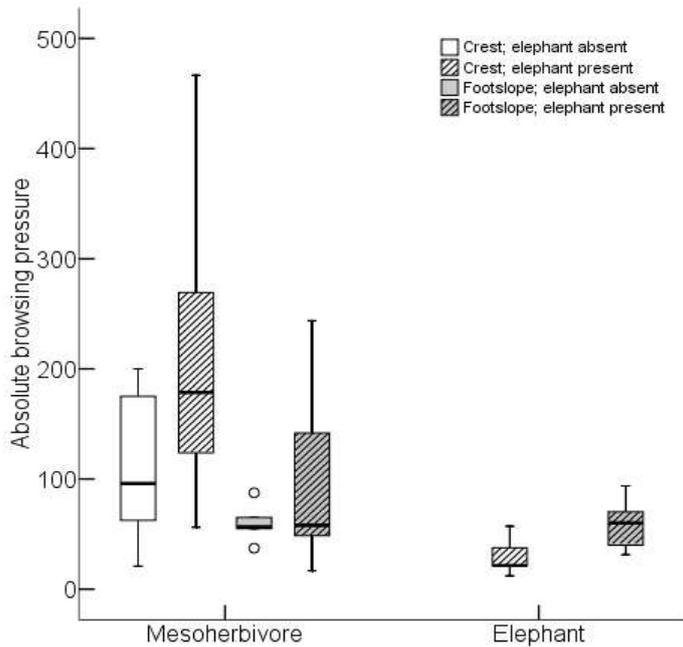
*Differences in browsing pressure*

Absolute browsing pressure of elephant on the 19 woody species was not significantly affected by slope position ( $P = 0.065$ ; Fig. 5). Absolute browsing pressure of mesoherbivores was also not significantly affected by slope position ( $P = 0.213$ ; Fig. 5), or by elephant presence ( $P = 0.191$ ) or site ( $P = 0.456$ ).

In Balule where elephant and mesoherbivores overlap, browsing pressure by mesoherbivores was significantly lower where elephant browsing pressure was higher (Fig. 6a;  $F_{1,8} = 6.661$ ,  $P_{(1-tailed)} = 0.017$ ,  $R^2 = 0.454$ ). When separated between slope positions, this negative relationship was only significant on crests (Fig. 6b;  $F_{1,3} = 8.327$ ,  $P_{(1-tailed)} = 0.032$ ,  $R^2 = 0.735$ ).

## **Discussion**

Slope position was an important spatial distinguishing feature that affected woody species richness, woody species assemblages and tree population structures in Balule Nature Reserve. Noticeably, slope position did not affect densities of any of the functional height classes (including the recruitment phase), or influence browsing pressure. Recruitment and regeneration seem to take place on both slope positions as well as in the presence and absence of elephant, as indicated by the frequency distributions. Although short-term (i.e., 4 years) elephant access did not affect woody species assemblages or species richness, elephant presence did affect tree population structures and densities in the sapling class. We also found that browsing by mesoherbivores was lower in areas with higher elephant browsing.

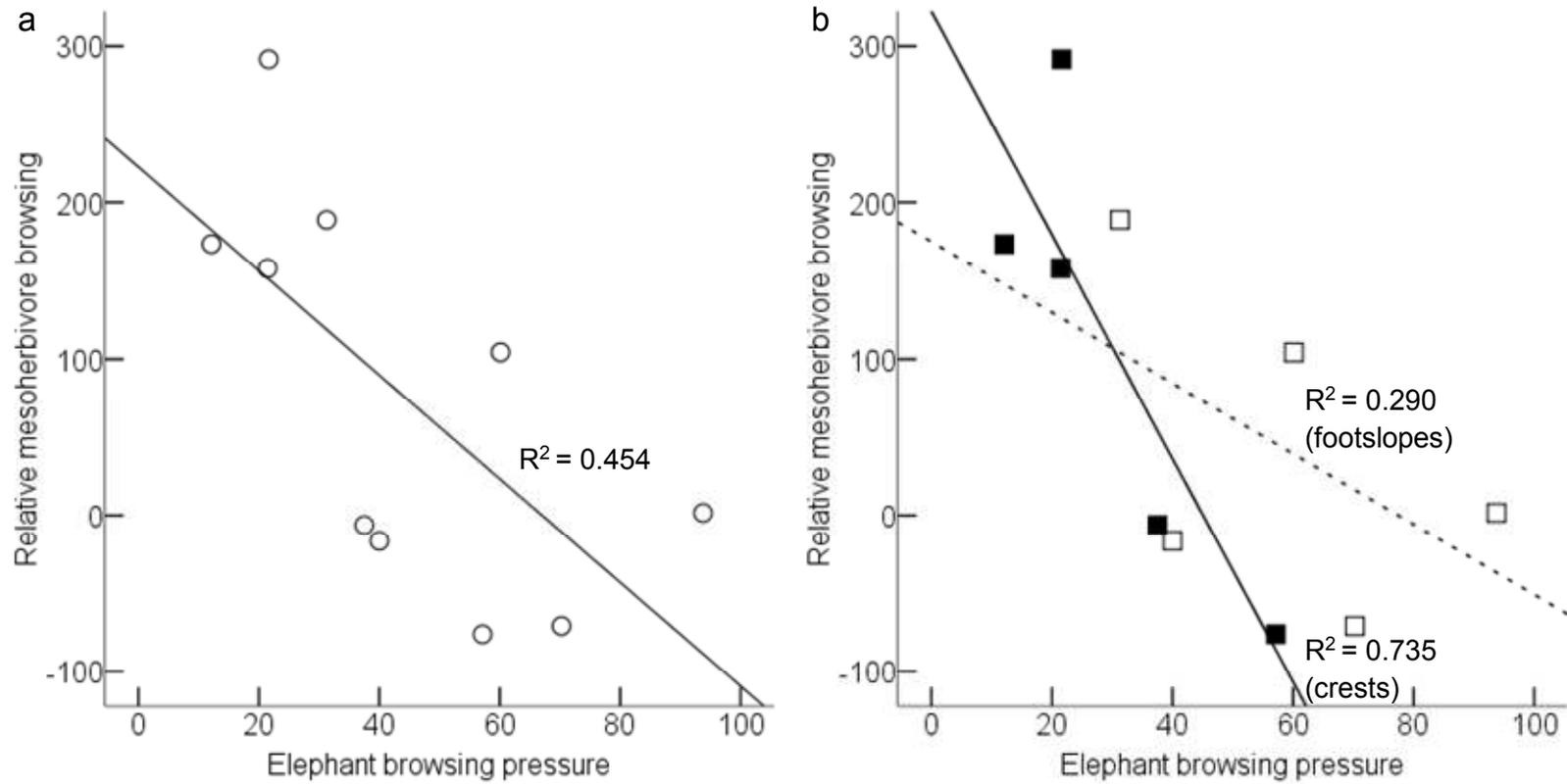


**Figure 5** No significant differences in absolute browsing pressure (number of browsing events) by mesoherbivores and elephant on the 19 plant species in the different treatments. Data are range (whiskers), 25 and 75 % quartiles (box), median (line) and circles are outlying values. N = 5 for each treatment.

#### *Effects of slope position*

In accordance with our expectation, slope position did affect woody species assemblages. The differences in species assemblages between slope positions were best explained by effective cation exchange capacity (ECEC), Zinc, sand (%) and clay (%) content. Species associated with higher soil concentrations of these nutrients were mainly less abundant species (e.g., *Acacia senegal*, *Balanites maughamii*, *Manilkara mochisia* and *Pappea capensis*). ECEC was highly correlated with Calcium and it may therefore be Calcium and not ECEC that was important in explaining the variation in species assemblages between the two slope positions.

Contrary to what we expected, slope position did not affect tree height distributions (including the recruitment phase), or direct browsing pressure. The spatial arrangements of vegetation patches on the hillslope typically affects the volume of run-off reaching the lower slope areas (Daws et al. 2002; Ludwig et al. 2005), which determines the increase in moisture and soil quality, and consequently the vegetation community (i.e., assemblages and structural characteristics). However, lower lying areas (i.e., bottomland or footslope) are not always more moist or higher in all soil nutrients than crests (Daws et al. 2002). Vegetation along the slope can effectively absorb



**Figure 6** The negative effect of higher elephant browsing on herbivory by mesoherbivores: (a) across all 10 plots in the elephant access area; (b) separately for footslopes (open squares, dashed line) and crests (filled squares, solid line) ( $N = 5$  sites for each slope position). Elephant browsing was measured as absolute browsing events. In order to account for among-site effects (i.e., local non-elephant density), relative browsing by mesoherbivore was calculated as the difference in absolute browsing events between Balule (elephant present) and Ukhozi (elephant absent) for each pair of corresponding quadrats.

the run-off, which appears to be the case within the Balule Nature Reserve and is substantiated by the absence of higher tree, stem and recruitment densities, or lack of higher browsing levels, on the footslopes. Therefore, unlike proposed in various studies (Ludwig et al. 2005; Grant and Scholes 2006; Jacobs et al. 2007), being situated at the lower part of the slope does not necessarily enhance growth of a woody individual or increase browsing levels.

The lack of differential elephant browsing pressure between footslopes and crests could therefore be due to similar tree densities on both slope positions (Barnes 1983), or the circadian movement pattern of elephant over the catenal gradient (De Knecht 2010). Elephant use the lower lying areas during midday when temperatures are high, while during night time they also utilise crests (De Knecht 2010). Thus, foraging impact can be spatially homogenous over the catena, as elephant forage up to 18 h daily (Owen-Smith 1988). Behavioural responses to temperature (Kinahan et al. 2007; De Knecht 2010) may thus outweigh responses to resource heterogeneity at this scale.

Despite the absence of significant differences in elephant browsing pressure between slope positions, there was a strong negative relationship between elephant browsing pressure and herbivory by mesoherbivores on crests, but less so on footslopes. This may indicate a strong response to the available resources by mesoherbivores on crests. Crests had a different species assemblage and lower species diversity compared to footslopes, and were thus likely to be more uniform in nutritional quality than footslopes. Our results add to the contrast of two recent studies focussing on herbivory effects at different productivity scales. Asner et al. (2009) found herbivore impact to be greater in high nutrient, lowland areas, than in upland areas in Kruger National Park, in close proximity to our study area. However, Pringle et al. (2007) found the opposite pattern in Kenya, where higher foraging was recorded on low productivity sites. We also found soil properties to differ between slope positions but these did not influence herbivory between slope positions within our study area. Such variation in herbivory responses across studies further illustrates the complexity of ecosystems and the dubious nature of generalising between different areas.

#### *Effects of elephant*

No effect of short-term elephant access (i.e., 4 years) was detected on species richness, woody species assemblages, and overall densities of trees and stems in Balule. In contrast, vegetation changes both from long and short-term elephant exclusion have been seen in a range of areas in Africa (Owen-Smith 1988; Augustine and McNaughton 2004; Levick and Rogers 2008;

Lagendijk et al. 2011b). Elephant densities in Balule could just have been too low to show an effect on species composition in the short term.

Although both slope position and elephant access per se did not have an effect on browsing by mesoherbivores, browsing pressure by mesoherbivores was lower at higher elephant browsing levels. Assuming that elephants spend more time in areas where their browsing pressure is higher, the reduced browsing by mesoherbivores can be interpreted either as behavioural displacement of mesoherbivores by elephants, or as competition, indicating that facilitation of elephants on mesoherbivore browsing through increased forage availability and quality does not occur. Furthermore, the possibility of behavioural displacement is substantiated by the greater number of saplings, which are within the feeding height range of mesoherbivores (see Du Toit 1990; Kirby et al. 2008), where elephants are present. Although elephants can facilitate mesoherbivores (Rutina et al. 2005; Makhabu et al. 2006; Kohi et al. 2011), we now also propose that elephant browsing activity can also displace mesoherbivores, similar to the findings of Lagendijk et al. (2011b) for elephants displacing nyala *Tragelaphus angasii* in Sand Forest. Elephant access to an area can thereby have a positive effect on sapling regeneration into taller size classes, and as such influence vegetation dynamics.

### *Conclusions and Implications*

Observed patterns in vegetation composition and herbivory along the hillslope gradient are complex to explain and understand due to the numerous interactions present between biotic and abiotic elements. We found differences in some soil properties (e.g., Phosphorus, Potassium, Magnesium, Copper and  $ECEC \approx Ca$ ) between the crest and the footslope but apart from soil properties, many other environmental variables such as hydrology, wind exposure and radiation could also contribute to the underlying mechanisms explaining differences in species assemblages, woody vegetation structure and herbivory between slope positions (Homeier et al. 2010). The contrasting results found by other studies (Daws et al. 2002; Pringle et al. 2007; Asner et al. 2009) show that the observed relationship between the spatial pattern on the hillslope scale and the ecological processes does not always hold. In addition to the spatial heterogeneity within regional landscapes, this variation between study areas emphasises the importance of acknowledging the local topography, and highlights the need for more site-specific management.

The absence of a direct elephant effect on woody species composition, tree densities and height structure is important to recognise, especially within the current 'elephant debate' in which

conservation managers are concerned with the effects of an increasing elephant population on the sustainability of protected areas (Kerley et al. 2008). Our observed lack of a direct effect of elephant browsing (with the exception of the population structures), as well as the facilitating effect for sapling recruitment, is in contrast to many studies of elephant impact. Published studies so far typically report negative effects (see Kerley et al. 2008), thus creating an unidirectional bias in our understanding of elephant effects at all spatial and temporal scales. It is thus imperative for elephant management that these non-significant as well as positive effects also get reported. Certainly, understanding the scale of elephant impacts is important; while there may not be a direct effect at the local hillslope scale in our study, there may be effects at larger landscape or temporal scales, especially under higher elephant densities.

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### **References**

- Asner GP, Levick S, Kennedy-Bowdoin T, Knapp DE, Emerson R, Jacobson J, Colgan MS, Martin RE. 2009. Large-scale impacts of herbivores on the structural diversity of African savannas. *PNAS* 106:4947-4952.
- Augustine DJ, McNaughton SJ. 2004. Regulation of shrub dynamics by native browsing ungulates on East African rangeland. *Journal of Applied Ecology* 41:45-58.
- Babweteera F, Savill P, Brown N. 2007. *Balanites wilsoniana*: Regeneration with and without elephants. *Biological Conservation* 134:40-47.
- Barnes RFW. 1983. Effects of elephant browsing on woodlands in a Tanzanian National Park: measurements, models and management. *Journal of Applied Ecology* 20:521-539.

- Belsky AJ. 1984. Role of small browsing mammals in preventing woodland regeneration in the Serengeti National Park, Tanzania. *African Journal of Ecology* 22:271-279.
- Boyes LJ, Griffiths ME, Manson AD, Lawes MJ. 2010. Soil nutrients are not responsible for arrested succession in disturbed coastal dune forest. *Plant Ecology* 208:293-305.
- Clarke KR, Warwick RM. 2001. Change in marine communities: an approach to statistical analysis and interpretation, 2nd edition edn. PRIMER-E, Plymouth, UK.
- Cowling RM, Kamineth A, Difford M, Campbell EE. 2009. Contemporary and historical impacts of megaherbivores on the population structure of tree euphorbias in South African subtropical thicket. *African Journal of Ecology* 48:335-345.
- Daws MI, Mullins CE, Burslem DFRP, Paton SR, Dalling JW. 2002. Topographic position affects the water regime in a semideciduous tropical forest in Panamá. *Plant and Soil* 238:79-90.
- de Garine-Wichatitsky M, Fritz H, Gordon IJ, Illius AW. 2004. Bush selection along foraging pathways by sympatric impala and greater kudu. *Oecologia* 141:66-75.
- De Knegt HJ. 2010. Beyond the here and now: herbivore ecology in a spatial-temporal context. PhD-thesis, Wageningen University, The Netherlands.
- Du Toit JT. 1990. Feeding-height stratification among African browsing ruminants. *African Journal of Ecology* 28:55-61.
- Du Toit JT. 2003. Large herbivores and savanna heterogeneity. In: du Toit JT, Rogers KH, Biggs HC eds *The Kruger Experience: Ecology and management of savanna heterogeneity*. Island Press, Washington, pp 292-309.
- Du Toit JT, Cumming DHM. 1999. Functional significance of ungulate diversity in African savannas and the ecological implications of the spread of pastoralism. *Biodiversity and Conservation* 8:1643-1661.
- Edkins MT, Kruger LM, Harris K, Midgley JJ. 2007. Baobabs and elephants in Kruger National Park: nowhere to hide. *African Journal of Ecology* 46:119-125.
- Ferguson CD. 1997. Environmental survey and management recommendations for Venice 40 KU. In, p Unpublished report.
- Fritz H, Duncan P, Gordon IJ, Illius AW. 2002. Megaherbivores influence trophic guilds structure in African ungulate communities. *Oecologia* 131:620-625.
- Grant CC, Scholes MC. 2006. The importance of nutrient hot-spots in the conservation and management of large wild mammalian herbivores in semi-arid savannas. *Biological Conservation* 130:426-437.

- Holdo RM, McDowell LR. 2004. Termite Mounds as Nutrient-Rich Food Patches for Elephants. *Biotropica* 36:231-239.
- Homeier J, Breckle S-W, Günter S, Rollenbeck RT, Leuschner C. 2010. Tree diversity, forest structure and productivity along altitudinal and topographical gradients in a species-rich Ecuadorian montane rain forest. *Biotropica* 42:140-148.
- Illius AW, O'Connor TG. 2000. Resource heterogeneity and ungulate population dynamics. *Oikos* 89:283-294.
- Jacobs SM, Bechtold JS, Biggs HC, Grimm NB, Lorentz S, McClain ME, Naiman RJ, Perakis SS, Pinay G, Scholes MC. 2007. Nutrient vectors and riparian processing: a review with special reference to African semiarid savanna ecosystems. *Ecosystems* 10: 1231-1249.
- Kalwij JM, de Boer WF, Mucina L, Prins HHT, Skarpe C, Winterbach C. 2010. Tree cover and biomass increase in a southern African savanna despite growing elephant population. *Ecological Applications* 20:222-233.
- Kerley GIH, Landman M, Kruger L, Owen-Smith N, Balfour D, de Boer WF, Gaylard A, Lindsay K, Slotow R. 2008. Effects of elephants on ecosystems and biodiversity. Scholes RJ, Mennell, KG, editors. *Elephant Management: A Scientific Assessment for South Africa*. Johannesburg: Witwatersrand University Press. p146-205.
- Kinahan AA, Pimm SL, Van Aarde J. 2007. Ambient temperature as a determinant of landscape use in the savanna elephant, *Loxodonta africana*. *Journal of Thermal Biology* 32:47-59.
- Kirby T, Shannon G, Page B, Slotow R. 2008. The influence of sexual dimorphisms on the foraging behaviour of the nyala *Tragelaphus angasii*. *Acta Zoologica Sinica* 54:561-568.
- Kohi EM, de Boer WF, Peel MJS, Slotow R, Van der Waal C, Heitkönig IMA, Skidmore AK, Prins H. 2011. African elephants *Loxodonta africana* amplify browse heterogeneity in African savannas. *Biotropica* DOI: 10.1111/j.1744-7429.2010.00724.x.
- Lagendijk DDG, Mackey RL, Page B, Slotow R. 2011a. The effects of herbivory by a mega- and mesoherbivore on tree recruitment in Sand Forest, South Africa. *PLoS ONE* 6:e17983.
- Lagendijk G, Page BR, Slotow R. 2011b. Short-term effects of single species browsing release by different-sized herbivores on Sand Forest vegetation community, South Africa. *Biotropica*:DOI: 10.1111/j.1744-7429.2011.00776.x.
- Levick S, Rogers K. 2008. Patch and species specific responses of savanna woody vegetation to browser exclusion. *Biological Conservation* 141:489-498.
- Ludwig JA, Wilcox BP, Breshears DD, Tongway DJ, Imeson AC. 2005. Vegetation patches and runoff-erosion as interacting ecohydrological processes in semiarid landscapes. *Ecology* 86:288-297.

- Lykke AM. 1998. Assessment of species composition change in savanna vegetation by means of woody plants' size class distributions and local information. *Biodiversity and Conservation* 7:1261-1275.
- Macandza VA, Owen-Smith N, Cross PC. 2004. Forage selection by African buffalo in the late dry season in two landscapes. *South African Journal of Wildlife Research* 34:113-121.
- Makhabu SW, Skarpe C, Hytteborn H. 2006. Elephant impact on shoot distribution on trees and on rebrowsing by smaller browsers. *Acta Oecologica* 30:136-146.
- Moe SR, Rutina LP, Hytteborn H, Du Toit JT. 2009. What controls woodland regeneration after elephants have killed the big trees? *Journal of Applied Ecology* 46:223-230.
- Nellemann C, Moe SR, Rutina LP. 2002. Links between terrain characteristics and forage patterns of elephants *Loxodonta africana* in northern Botswana. *Journal of Tropical Ecology* 18:835-844.
- Obiri JAF, Lawes MJ, Mukolwe M. 2002. The dynamics and sustainable use of high-value tree species of the coastal Pondoland forests of the Eastern Cape Province, South Africa. *Forest Ecology and Management* 166:131-148.
- Owen-Smith RN. 1988. Megaherbivores: the influence of very large body size on ecology. Cambridge: Cambridge University Press. 369p.
- Peel M. 2007. Ecological Monitoring: Association of Private Nature Reserves Timbavati, Umbabat, Klaserie and Balule. In. Agricultural Research Council, Nelspruit.
- Pringle RM, Young TP, Rubenstein DI, McCauley DJ. 2007. Herbivore-initiated interaction cascades and their modulation by productivity in an African savanna. *PNAS* 104:193-197.
- Prins HHT, Iason GR. 1989. Dangerous lions and nonchalant buffalo. *Behaviour* 108 : 262-296.
- Prins HHT, van der Jeugd HP. 1993. Herbivore Population Crashes and Woodland Structure in East Africa. *Journal of Ecology* 81:305-314.
- Prins HHT, Van Langevelde F. 2008. Assembling a diet from different places. In: Prins HHT, Van Langevelde F eds *Resource Ecology: Spatial and Temporal Dynamics of Foraging*. Springer, pp 129-155.
- Rutina LP, Moe SR, Swenson JE. 2005. Elephant *Loxodonta africana* driven woodland conversion to shrubland improves dry-season browse availability for impalas *Aepyceros melampus*. *Wildlife Biology* 11:207-213.
- Seagle SW, McNaughton SJ. 1992. Spatial variation in forage nutrient concentrations and the distribution of Serengeti grazing ungulates. *Landscape Ecology* 7:229-241.

- Shannon G, Druce DJ, Page BR, Eckhardt HC, Grant R, Slotow R. 2008. The utilization of large savanna trees by elephant in southern Kruger National Park. *Journal of Tropical Ecology* 24:281-289.
- Smit I, Grant CC, Devereux BJ. 2007. Do artificial waterholes influence the way herbivores use the landscape? Herbivore distribution patterns around rivers and artificial surface water sources in a large African savanna park. *Biological Conservation* 136:85-99.
- Thaker M, Vanak AT, Owen CR, Ogden MB, Niemann SM, Slotow R. 2011. Minimizing predation risk in a landscape of multiple predators: effects on the spatial distribution of African ungulates. *Ecology* 92:398-407.
- Valeix M, Chamaillé-Jammes S, Fritz H. 2007. Interference competition and temporal niche shifts: elephants and herbivore communities at waterholes. *Oecologia* 153:739-748.
- Walker BH, Stone L, Hederson L, Verner M. 1986. Size structure analysis of the dominant trees in a South African savanna. *South African Journal of Botany* 52:397-402.
- Weyerhaeuser FJ. 1985. Survey of elephant damage to baobabs in Tanzania's Lake Manyara National Park. *African Journal of Ecology* 23:235-243.
- Whyte IJ, Biggs HC, Gaylard A, Braack LEO. 1999. A new policy for the management of the Kruger National Park's elephant population. *Koedoe* 42:111-132.
- Wronski T. 2002. Feeding ecology and foraging behaviour of impala *Aepyceros melampus* in Lake Mburo National Park, Uganda. *African Journal of Ecology* 40:205-211.

## **CHAPTER 4**

### **The Effects of Herbivory by a Mega- and Mesoherbivore on Tree Recruitment in Sand Forest, South Africa**

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**Abstract**

Herbivory by megaherbivores on woody vegetation in general is well documented; however studies focusing on the individual browsing effects of both mega- and mesoherbivore species on recruitment are scarce. We determined these effects for elephant *Loxodonta africana* and nyala *Tragelaphus angasii* in the critically endangered Sand Forest, which is restricted to east southern Africa, and is conserved mainly in small reserves with high herbivore densities. Replicated experimental treatments (400 m<sup>2</sup>) in a single forest patch were used to exclude elephant, or both elephant and nyala. In each treatment, all woody individuals were identified to species and number of stems, diameter and height were recorded. Results of changes after two years are presented. Individual tree and stem densities had increased in absence of nyala and elephant. Seedling recruitment (based on height and diameter) was inhibited by nyala, and by elephant and nyala in combination, thereby preventing recruitment into the sapling stage. Neither nyala or elephant significantly reduced sapling densities. Excluding both elephant and nyala in combination enhanced recruitment of woody species, as seedling densities increased, indicating that forest regeneration is impacted by both mega- and mesoherbivores. The Sand Forest tree community approached an inverse J-shaped curve, with the highest abundance in the smaller size classes. However, the larger characteristic tree species in particular, such as *Newtonia hildebrandtii*, were missing cohorts in the middle size classes. When setting management goals to conserve habitats of key importance, conservation management plans need to consider the total herbivore assemblage present and the resulting browsing effects on vegetation. Especially in Africa, where the broadest suite of megaherbivores still persists, and which is currently dealing with the 'elephant problem', the individual effects of different herbivore species on recruitment and dynamics of forests and woodlands are important issues which need conclusive answers.

## Introduction

Different-size herbivores have different feeding preferences (de Garine-Wichatitsky et al. 2004); however, some overlap, and hence competition, might exist between different trophic guilds (Fritz et al. 2002). Megaherbivores (body mass  $\geq 1000$  kg (Owen-Smith 1988)) compete with mesoherbivores (medium-size herbivores with body mass between 50 and 450 kg (Fritz et al. 2002; de Garine-Wichatitsky et al. 2004)) for food (Fritz et al. 2002) as they feed in overlapping height ranges (Lagendijk 2003; Kirby et al. 2008). Through their browsing activities, both mega- and mesoherbivores have the capacity to alter structural diversity (e.g. height class distributions) of forests and woodlands (Eckhardt et al. 2000; Augustine and McNaughton 2004). Some megaherbivores open up the canopy by changing the vertical structure from top down, by impacting on large trees and browsing at higher levels (Owen-Smith 1988). On the other hand, mesoherbivores may have considerable effects as (1) controllers of the state induced by megaherbivores, by suppressing woodland or forest recovery through browsing after megaherbivore impact has altered woodland to shrubland (Pickett et al. 2003) or (2) top down control of recruitment into taller height classes by browsing of seedlings (Belsky 1984; Prins and Van der Jeugd 1993). Individual species or entire communities may disappear over time when there is no adequate recruitment and hence regeneration into taller height classes to compensate natural die-offs, impact of fire (Dublin et al. 1990) and megaherbivores.

While numerous studies have focused on megaherbivore impact on woody communities (e.g. Owen-Smith 1988; Ben-Shahar 1998; Hawthorne and Parren 2000; Gadd 2002; Jacobs and Biggs 2002; Shannon et al. 2008), and on the effects of herbivores in general on community structure and composition (Burke 1997; Bergquist et al. 1999; Cadenasso et al. 2002; Merrill et al. 2003; Levick and Rogers 2008), the combined effects of both mega- and mesoherbivore species on different height classes have received scant attention. Exclosure experiments in savanna landscapes have tried to separate effects on vegetation by different groups of herbivores (Shaw et al. 2002; Goheen et al. 2004, 2007; Hagenah 2006; Riginos and Young 2007; Siebert and Eckhardt 2008). However, effects observed in these studies can not be positively ascribed to one species only, when distinguishing between groups of herbivores of similar sizes. Consequently, the specific browsing effects of both mega- and mesoherbivores on regeneration of woody vegetation, especially in the African context where the broadest suite of megaherbivores still persists, still remain largely unknown.

Here we focus on the impacts on seedling and sapling recruitment by a mega- and mesoherbivore within the critically endangered Sand Forest community (Mucina and Rutherford 2006). This deciduous dry forest type is restricted to the Maputaland Centre of Endemism in north-eastern KwaZulu-Natal, South Africa and southern Mozambique (Kirkwood and Midgley 1999; Matthews et al. 2001; Siebert et al. 2004). Sand Forest generally occurs in a mosaic of patches enclosed by mixed woodland or savanna bushveld (Matthews 2005; Kellerman and Van Rooyen 2007), and includes a large number of rare and endemic species (Matthews et al. 2001; Siebert et al. 2004; Kellerman and Van Rooyen 2007). Its restricted geographic range and unique species composition makes Sand Forest one of the most important habitat types for conservation in southern Africa (Moll 1980; Kirkwood and Midgley 1999; Matthews 2005). Sand Forest is susceptible to fire and selective species utilisation by both man and herbivores, the effects of which are exacerbated by Sand Forest's low resilience to disturbance and poor recruitment rates of its tree species (Matthews et al. 2001; Botes et al. 2006; Gaugris et al. 2008). While foraging, browsing herbivores create pathways which open up the forest (Kerley et al. 2008; Shannon et al. 2009). Once savanna vegetation enters these gaps within the Sand Forest, successive changes to savanna woodland may be irreversible (Matthews 2005; Botes et al. 2006).

The dynamics of Sand Forest are poorly understood (Kellerman and Van Rooyen 2007). The structural diversity in the Sand Forest system in some protected areas has changed drastically over the past decade, particularly in Tembe Elephant Park (Matthews pers. comm.) and Phinda Private Game Reserve (Pretorius pers. comm.). The main reason for this is thought to be herbivory (Repton 2007; Kirby et al. 2008), affecting both the recruitment phase and taller height classes. Both elephant *Loxodonta africana* and nyala *Tragelaphus angasii* became locally abundant in protected Sand Forest areas after (re)introductions of these species in the early 1990s.

Conservation of the Sand Forest community is of critical importance, and it is therefore imperative to assess potential drivers affecting the tree community and its low recruitment rates. Management questions have been raised regarding the impact of herbivores, in particular elephants (Owen-Smith et al. 2006), on the vegetation, such as whether elephants or other herbivores are causing irreversible damage to the Sand Forest ecosystem, and if densities of these species need to be reduced in order to conserve the forest. We hypothesise that both mixed feeders have had, and are having, substantial impact on the vegetation (Matthews et al. 2001; Repton 2007; Kirby et al. 2008), as densities of both elephant and nyala have increased since (re)introduction with concomitant changes to Sand Forest structural diversity. Therefore, the aim

of this study was to assess the role of elephant and nyala on Sand Forest structure through their individual and combined browsing effect, particularly on recruitment. While impala *Aepyceros melampus* have been linked to recruitment limitation (Prins and Van der Jeugd 1993; Moe et al. 2009), this has not been studied for nyala. To our knowledge, this is the first study to experimentally separate the browsing effects of a mega- and mesoherbivore.

## Methods

### *Study area*

Phinda Private Game Reserve (hereafter Phinda) is a 180 km<sup>2</sup> (27°92' - 27°68' S; 32°44' - 32°20' E) conservation area in Maputaland, northern KwaZulu-Natal, South Africa. The reserve includes a wide range of habitat types, such as western Maputaland sandy bushveld as well as several patches of the endemic Sand Forest (Mucina and Rutherford 2006). The climate is subtropical with hot, humid summers and warm, dry winters. Temperatures range from a minimum of 10°C in winter to a maximum of 35°C in summer. Annual rainfall ranges between 350 mm and 1100 mm, and varies spatially from west to east.

Before Phinda was created in 1991, the area consisted of private and small game farms. Game was introduced following the establishment of the park (Repton 2007), with fifty-eight elephants being released into Phinda between 1992 and 1994 (Druce et al. 2006). At the start of this study (2005) 81 elephants were present in the reserve, increasing to 98 individuals in 2007 (based on an individually identified and monitored elephant population (e.g. Druce et al. 2008)). Nyala numbered approximately 1100 and 1750 individuals in 2005 and 2007, respectively (based on annual aerial game counts). Other browsing ungulates in Phinda include giraffe *Giraffa camelopardalis* (154), kudu *Tragelaphus strepsiceros* (188), impala (1690), red duiker *Cephalophus natalensis* (23), common duiker *Sylvicapra grimmia* (no count available) and suni *Neotragus moschatus* (no count available). Counts in parentheses are approximate and reflect the 2007 annual helicopter game count.

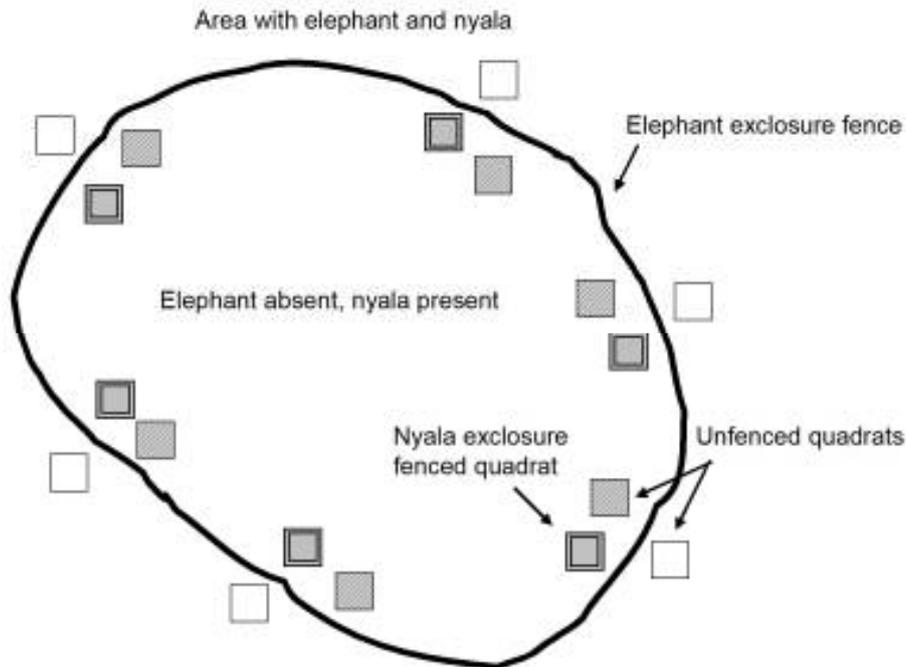
This study was conducted in the endemic Sand Forest, which occurs in the northern section of Phinda. Sand Forests occur on acidic, sandy soils with very little clay (Matthews et al. 2001). The Sand Forest is a dense vegetation type, with a closed canopy, 5 to 12 m high, without a significant understorey. Characteristic woody species include *Balanites maughamii*, *Cleistanthus schlechteri*, *Cola greenwayi*, *Croton pseudopulchellus*, *Dialium schlechteri*, *Drypetes arguta*,

*Hymenocardia ulmoides*, *Newtonia hildebrandtii* and *Pteleopsis myrtifolia* (Kirkwood and Midgley 1999; Matthews 2005; Moll 1980). Few mammal species utilise Sand Forest (Matthews 2005). In Phinda, elephant and nyala are the *only* mega- and mesoherbivore utilising the Sand Forest patches (Lagendijk pers. obs.).

#### *Experimental design*

The effects of elephant and nyala on Sand Forest recruitment were tested using exclosures. In November 2005, elephants were excluded from part of the Sand Forest using electrified (7000 volts per second) high tension galvanized wires (2.4 mm thick) erected at 1.8 m and 2 m above the ground, enclosing 3.09 km<sup>2</sup> of the 5.2 km<sup>2</sup> Sand Forest patch (Fig. 1). To determine the effects of both elephant and nyala separately, twelve exclosures of 20 m x 20 m using 1.8 m high bonnox fencing (a coarse wire mesh with 30 x 20 cm openings) were erected inside the elephant-free area. This type of fencing allowed passage for small-size herbivores such as duiker and suni, but excluded nyala. Adjacent to this exclosure, another 20 m x 20 m area was marked out and opposite these two treatments just outside the elephant fence a third 20 m x 20 m area was marked for sampling. This resulted in an experimental design of a set of three 400-m<sup>2</sup> treatments in close proximity, consisting of: (1) unfenced area available to all herbivores (open access “+E+N”); (2) area fenced to exclude only elephant (partial exclosure, nyala present “-E+N”); (3) area fenced to exclude both nyala and elephants (full exclosure “-E-N”), but providing access to smaller herbivores. There were a total of 12 replicates of this set of three treatments. Distance between replicates ranged between 0.12 km and 2.75 km.

A base-line study was conducted in 2005. In each quadrat (n = 36) all woody individuals (including seedlings; > 0.02 m and ≤ 0.5 m tall; and saplings, > 0.05 m and ≤ 1.5 m tall) were identified to species and counted. Diameters above the buttress swelling of all stems (including seedlings and saplings) and all tree heights were recorded. Diameters and the heights of trees to 2 m were measured, the heights of trees between 2 m and 4 m estimated to the nearest 20 cm, and the heights of taller trees estimated to the nearest 50 cm using the height of an observer as a scale following Shannon et al. (2008). Two years after implementation of the experiment, quadrats were sampled again during June – July or November – December 2007, with the three treatments from a replicate being sampled during the same sampling trip. Five open access plots were repositioned in 2007, therefore when doing pair-wise comparisons between the two sampling years, only 7 open access plots (+E+N) were included in the analyses. The analyses are of 2007 data unless otherwise stated.



**Figure 1** A schematic representation of the enclosure experiment with the three treatments: (1) open access, accessible for all herbivores (+E+N, open bars); (2) partial enclosure, elephant excluded, nyala present (-E+N, diagonal hatching); (3) full enclosure, both elephant and nyala excluded (-E-N, grey bars) (not to scale). The sets of three treatments were replicated 12 times.

### *Statistical analyses*

Following recommendations by Clarke and Warwick (2001), tree species contributing less than 4 percent of the abundance per plot in 2005 were discarded and only species present in both sampling years were included. Given that recruitment is dependent on a local seed source, we believe that excluding the rare species provides a more robust test of recruitment patterns across treatments. Consequently a total of 26 tree species were included in the analyses (Table 1); all of these species were browsed upon by the herbivore guild during the course of the experiment.

Because there are two possible demographic responses to browsing viz. mortality or a coppicing response (i.e. the production of new stems after the terminal part of the main stem has been removed (Smallie and O'Connor 2000)), changes in both the density of individual trees (which measures mortality, but also reflects recruitment) and stem density (which measures the coppicing response or mortality of vertical stems) were investigated. Individual and stem densities were

**Table 1** List of 26 species included in the analyses

<i>Cola greenwayi</i> Brenan	<i>Monodora junodii</i> Engl. & Diels
<i>Combretum celastroides</i> Welw. Ex Laws.	<i>Newtonia hildebrandtii</i> (Vatke) Torre
<i>Combretum mkuzense</i> Carr & Retief	<i>Ptaeroxylon obliquum</i> (Thunb.) Radlk.
<i>Croton pseudopulchellus</i> Pax	<i>Pteleopsis myrtifolia</i> (Laws.) Engl. & Diels
<i>Croton steemkampianus</i> Gerstner	<i>Rhus gueinzii</i> Sond.
<i>Dialium schlechteri</i> Harms	<i>Rhus natalensis</i> Bernh. Ex Krauss
<i>Drypetes arguta</i> (Muell. Arg.) Hutch	<i>Salacia leptoclada</i> Tul.
<i>Grewia microthyrsa</i> K. Schum. Ex Burret	<i>Strychnos henningsii</i> Gilg
<i>Haplocoelum gallense</i> (Engl.) Radlk.	<i>Toddalopsis bremekampii</i> Verdoorn
<i>Hymenocardia ulmoides</i> Oliv.	<i>Tricalysia junodii</i> (Schinz) Brenan
<i>Hyperacanthus amoenus</i> (Sims) Bridson	<i>Uvaria caffra</i> E. Mey. Ex Sond.
<i>Landolphia kirkii</i> T.-Dyer	<i>Wrightia natalensis</i> Stapf
<i>Monanthes caffra</i> (Sond.) Verdc.	<i>Zanthoxylum</i> sp.

scaled up from 400 m<sup>2</sup> to 1 ha. Individual trees and stems were allocated to seven height classes ( $\leq 0.5$  m, 0.51 -1.5 m, 1.51 – 3 m, 3.01 – 5 m, 5.01 - 8 m, 8.01-12 m, >12 m), which roughly correspond to the limits at which browsing by different-size herbivores occurs.

ANOVAs were used to test for differences in overall tree and stem densities among treatments in 2007, for which data were pooled for all species and height classes. Differences in seedling ( $\geq 0.02$  and  $\leq 0.5$  m in height) and sapling ( $> 0.5$  m and  $\leq 1.5$  m in height) abundance, as well as stem densities in these height classes, among treatments were also analysed using ANOVA. Pair-wise comparisons of individual overall tree densities and seedlings per treatment between 2005 and 2007 were also analysed using ANOVA.

Tree populations are regenerating when the population structure displays an inverse J-shaped frequency distribution (Lykke 1998; Obiri et al. 2002). This translates to a relatively high abundance of seedlings, which represents sufficient recruitment, and a relatively low abundance of tall trees. A distribution of a different shape is indicative of disturbance (Walker et al. 1986). Following previous work in Sand Forest (Everard et al. 1995; Van Wyk et al. 1996), we used 18 different size classes with 1 cm intervals to 7 cm diameter, thereafter 2 cm intervals to 15 cm diameter, 5 cm intervals to 30 cm diameter and 10 cm intervals to 60 cm. The diameter limits that are equivalent to the height categories we used are 1, 4, 9, 15, 25, 40 and > 40 cm diameter

(derived from a quadratic regression of diameter vs. height for all Sand Forest species ( $r^2 = 0.73$ )). A G-test was used to determine whether size distributions differed among treatments for the pooled data. To prevent compounding of Type 1 errors from running three pair-wise G-tests, alpha of 0.05 was Bonferroni-adjusted to 0.017.

At the tree species level, we focused our analyses on the three most common Sand Forest species in our study area (*Salacia leptoclada*, *Uvaria caffra* and *Tricalysia junodii*) and on three characteristic Sand Forest trees (*D. schlechteri*, *N. hildebrandtii* and *P. myrtifolia*) to determine the effect of elephant and/or nyala on recruitment. Seedling and sapling abundance were analysed separately among treatments per focus species using a two-way ANOVA. When ANOVA assumptions were not met, densities were analysed with a Kruskal-Wallis test. Size class distributions (SCD), which reflect population structures, were analysed for each of these six species using linear regressions (cf. (Lykke 1998; Condit et al. 1998)). Data were pooled per treatment. The number of individual trees per diameter class was divided by the width of the diameter class, giving an average density ( $D_i$ ) for the class midpoint ( $M_i$ ). These variables were ‘ $\ln + 1$ ’ – transformed prior to regression analyses. All size classes up to the largest size class containing individuals were included in the analyses. We used SCD slopes to interpret population structures. An inverse J-shaped curve is represented by a steep negative slope, while species with little regeneration show a negative slope close to zero.

For all the abovementioned statistical tests the significance level was set at  $P = 0.05$ , unless otherwise stated. All significant ANOVAs (assumptions of normality and homoscedasticity being met) were followed-up with Tukey’s post-hoc tests. All statistical analyses were performed using SPSS 15.0 (SPSS Inc., Chicago, USA).

## Results

In 2005, 12638 individual plants from 95 woody species, and in 2007, 17825 individual trees and 143 woody species were recorded in all treatments. In 2007, the dominant Sand Forest species *S. leptoclada*, *T. junodii*, and *U. caffra* made up 49.9% of all trees, compared to 53.4% in 2005.

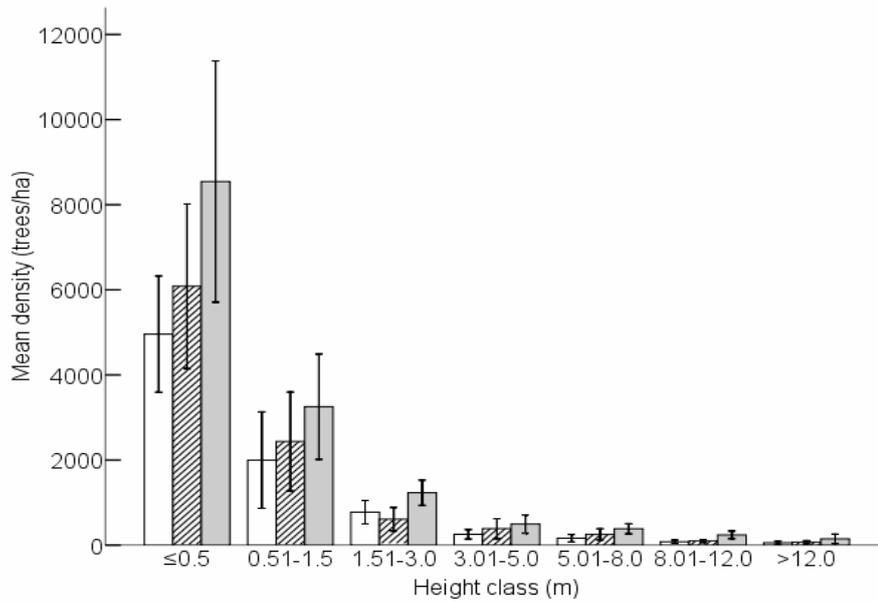
The twelve replicates of the experiment were considered to be homogeneous in 2005 as, when only taking the more abundant species ( $n = 26$ ) into account, there were no significant differences among treatments for the seedling ( $F_{0.05(2)2,33} = 0.363$ ,  $P = 0.698$ ), sapling ( $F_{0.05(2)2,33} = 0.944$ ,  $P = 0.399$ ), and overall (i.e. all size classes combined) tree and stem densities ( $F_{0.05(2)2,33} = 0.842$ ,  $P =$

0.440 and  $F_{0.05(2)2,33} = 1.905$ ,  $P = 0.165$  respectively). Note that when all species present were included in this analysis, there were still no significant differences for any of these contrasts (seedling:  $F_{0.05(2)2,33} = 1.044$ ,  $P = 0.363$ ; sapling:  $F_{0.05(2)2,33} = 0.758$ ,  $P = 0.464$ ; tree density for all size classes combined:  $F_{0.05(2)2,33} = 0.883$ ,  $P = 0.444$ ; stem density for all size classes combined:  $F_{0.05(2)2,33} = 2.734$ ,  $P = 0.080$ ).

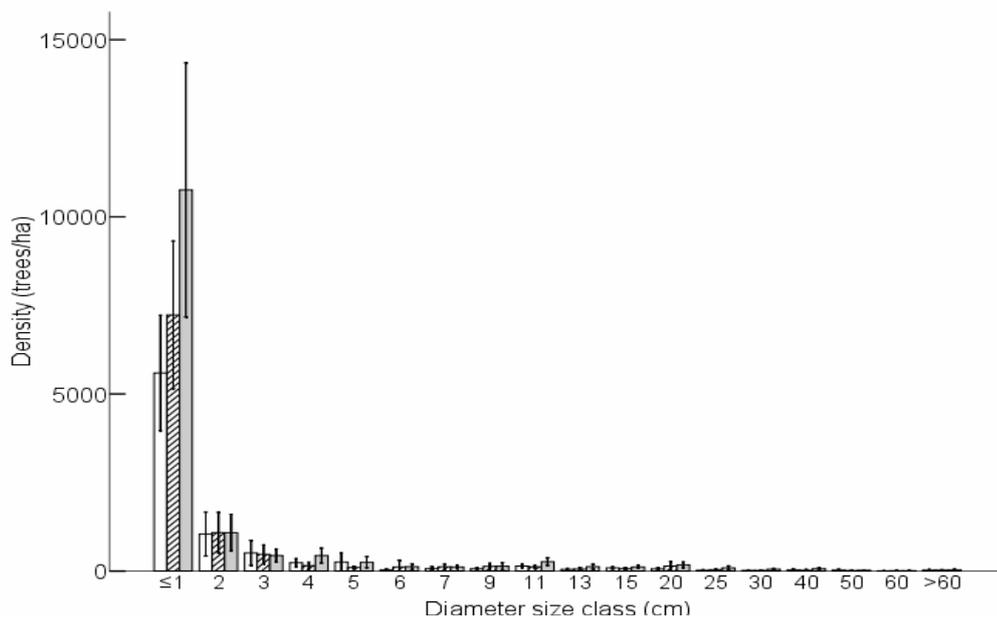
In contrast to this, for the 26 species in 2007 there were significant differences among the treatments in both the overall tree densities ( $F_{0.05(2)2,33} = 5.180$ ,  $P = 0.011$ ) and the overall stem densities ( $F_{0.05(2)2,33} = 4.426$ ,  $P = 0.020$ ), with densities in the full enclosure (-E-N) being significantly greater than in the open access treatment (+E+N) (overall tree density, Tukey:  $P = 0.010$ ; overall stem density, Tukey:  $P = 0.027$ ). The overall abundance of individual trees in the partial enclosure (-E+N), were not significantly different from those in the open access (+E+N) or in the full enclosure (-E-N) treatment. However stem densities were greater in the full enclosure than in the partial enclosure, although this was marginally not significant (Tukey:  $P = 0.056$ ). Pair-wise comparisons between 2005 and 2007 showed a significant increase in the full enclosure for overall tree densities (-E-N:  $F_{0.05(2)1,22} = 7.387$ ,  $P = 0.013$ ). Differences in overall stem densities per treatment between 2005 and 2007 were not significant (open access (+E+N):  $F_{0.05(2)1,12} = 0.599$ ,  $P = 0.454$ ; partial enclosure (-E+N):  $F_{0.05(2)1,22} = 0.537$ ,  $P = 0.471$ ; full enclosure (-E-N):  $F_{0.05(2)1,22} = 2.401$ ,  $P = 0.136$ ). This indicated that recruitment was taking place within the full enclosure (-E-N).

Seedling density of the 26 species differed significantly among treatments in 2007 ( $F_{0.05(2)2,33} = 3.582$ ,  $P = 0.039$ ; Fig. 2). Seedling densities in the full enclosure (-E-N) were significantly higher than in the open access (+E+N) treatment (Tukey:  $P = 0.035$ ), indicating that both nyala and elephant in combination reduced seedling densities. This is concordant with analysing seedling densities by tree diameter class as opposed to height class. Seedling density (0-1 cm diameter class) differed significantly among treatments ( $F_{0.05(2)2,33} = 5.104$ ,  $P = 0.012$ ), with greater seedling densities in the full enclosure (-E-N) than in the open access treatment (+E+N: Tukey:  $P = 0.010$ ; Fig. 3).

For the 26 species, pair-wise comparisons of seedling ( $\leq 0.5$  m in height) density between 2005 and 2007 was not significantly different within the partial enclosure (-E+N:  $F_{0.05(2)1,22} = 3.186$ ,  $P = 0.088$ ). However, there was a significant increase in seedling densities in the open access



**Figure 2** Mean density (trees/ha) per height class (i.e. seedlings:  $\leq 0.5$  m; saplings; 0.51 – 1.5 m) for all 26 species combined per treatment. Open access (+E+N, open bars), partial exclusion (-E+N, diagonal hatching) and full exclusion (-E-N, grey bars). The bars indicate 95% confidence intervals of the means. N = 12 replicates per treatment.



**Figure 3** Mean density (trees/ha) per diameter size class (i.e. seedlings:  $\leq 1$  cm; saplings; 1 – 4 cm) for all 26 species combined per treatment. Open access (+E+N, open bars), partial exclusion (-E+N, diagonal hatching) and full exclusion (-E-N, grey bars). The bars indicate 95% confidence intervals of the means. N = 12 replicates per treatment.

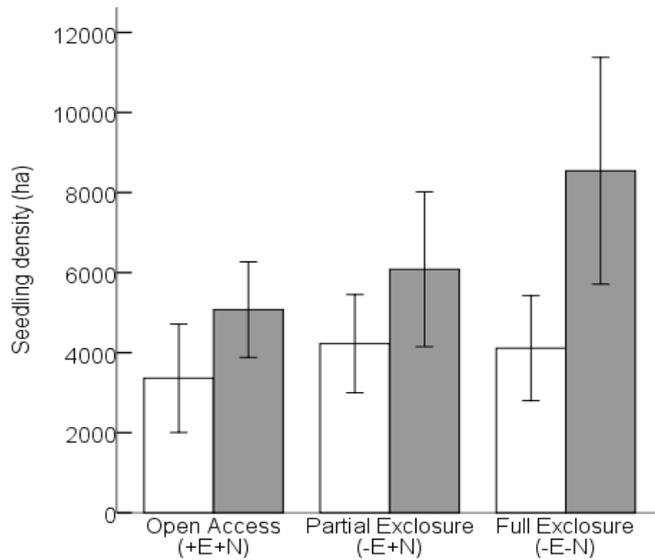
treatment (+E+N:  $F_{0.05(2)1,12} = 5.386$ ,  $P = 0.039$ ) and the full enclosure between 2005 and 2007 (-E-N:  $F_{0.05(2)1,22} = 9.755$ ,  $P = 0.005$ ; Fig. 4).

For the 26 species, sapling densities in 2007 were not significantly different among treatments ( $F_{0.05(2)2,33} = 1.421$ ,  $P = 0.256$ ; Fig. 2), and there were no significant differences in sapling densities within each treatment between the two sampling years ( $P > 0.21$ ). Using stem diameter as opposed to height, there were also no significant differences in densities of saplings (1.01 to 4 cm diameter class) among treatments in 2007 ( $F_{0.05(2)2,33} = 0.123$ ,  $P = 0.884$ ; Fig. 3).

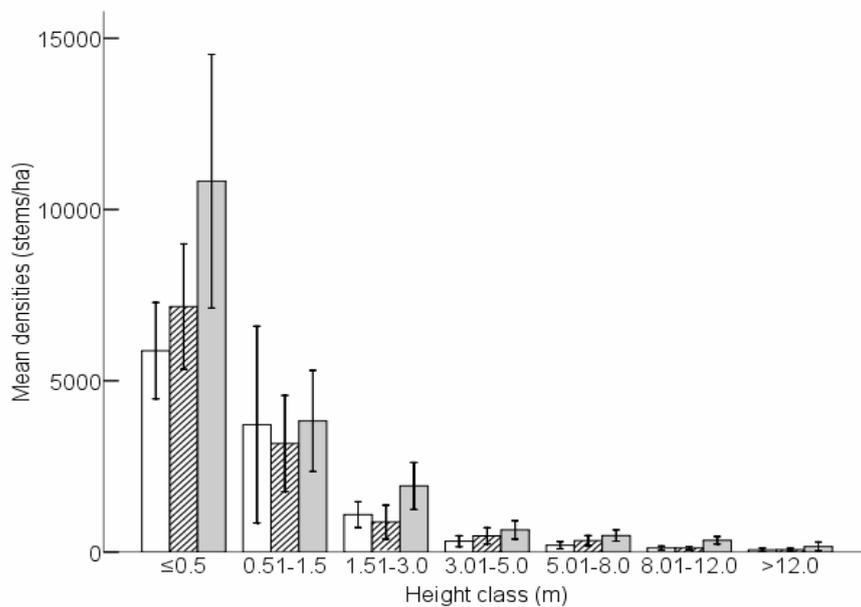
Seedling stem densities in 2007 were significantly different among the three treatments ( $F_{0.05(2)2,33} = 5.030$ ,  $P = 0.012$ ; Fig. 5), with seedling stem densities significantly greater in the full enclosure (-E-N) (Tukey:  $P = 0.012$ ) than the open access treatment (+E+N). Sapling stem densities were not significantly different among treatments ( $F_{0.05(2)2,33} = 0.146$ ,  $P = 0.865$ ; Fig. 5). The greater seedling stem densities in the full enclosure also indicate that the differences in the density of individual trees are mostly due to recruitment of individual trees. However, additional stems were added from the recruitment of multi-stemmed trees or from the production of new stems from coppicing as a response to browsing prior to the establishment of the experiment.

Population structures were assessed using diameter size distributions for all species combined. In 2007, diameter size distributions were significantly different among treatments ( $G_{12} = 3169$ ,  $P \leq 0.017$  for all pair-wise comparisons). In all treatments, the highest abundance was found in the smallest size ( $\leq 1.0$  cm) class (Fig. 3). Population structures approached an inverse J-shaped curve.

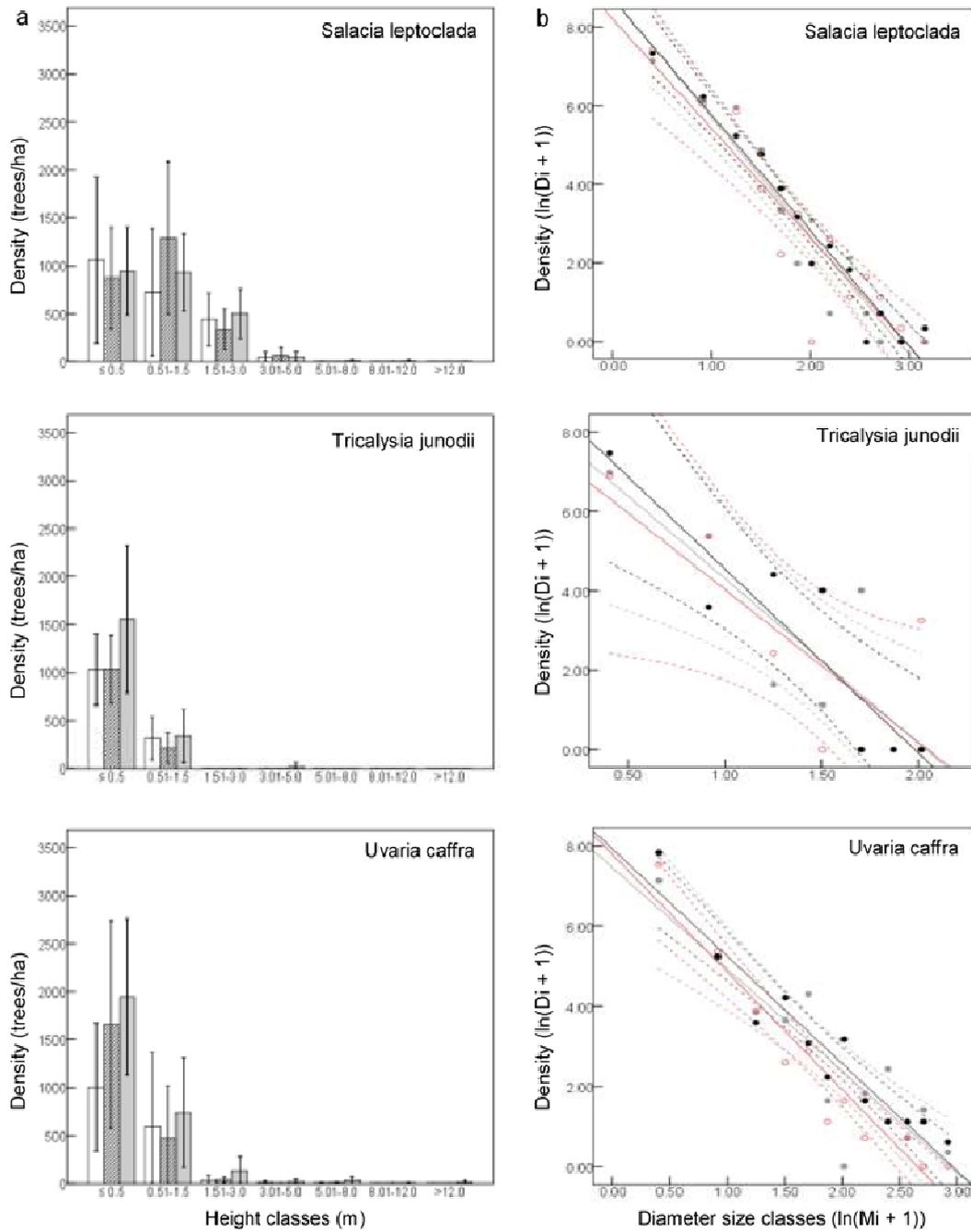
Both seedling and sapling densities of each of the six selected focus species did not significantly differ among treatments (seedlings:  $P > 0.54$ ; saplings:  $P > 0.33$ ; Fig. 6a, 7a). However, the population structures of each of these six species had missing diameter size classes (mainly middle size classes). The population structures of *S. leptoclada*, *U. caffra* and *T. junodii* approached the inverse J-shaped curve characteristic of increasing populations, which is supported by the strong negative SCD slopes for these species (Fig. 6b, 7b, Appendix S4.1). *D. schlechteri*, *N. hildebrandtii* and *P. myrtifolia* showed a SCD slope closer to zero, indicating a disruptive population structure with little regeneration. However this was not significant for *N. hildebrandtii* (in any of the treatments) and *D. schlechteri* (in the full enclosure (-E-N)).



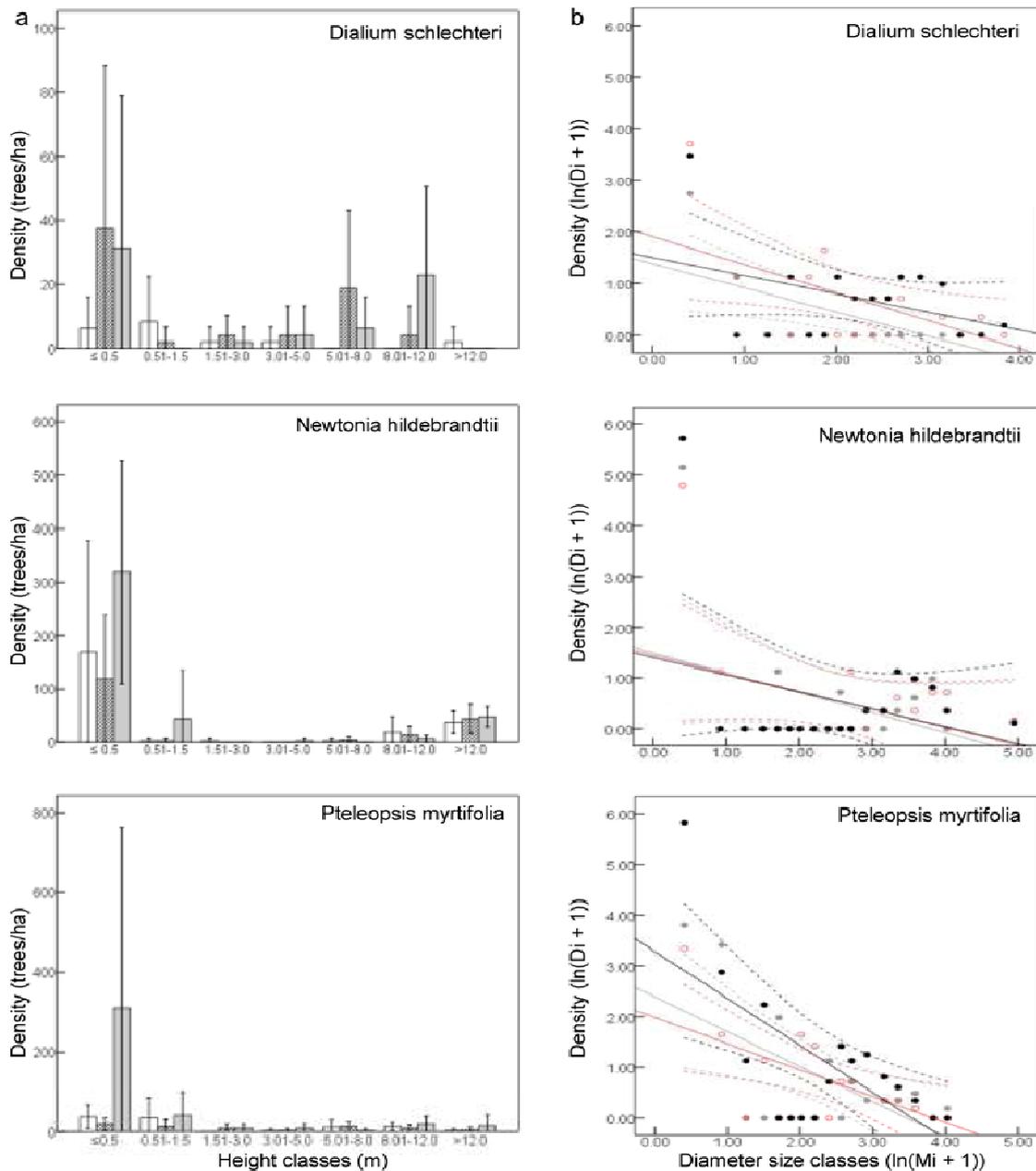
**Figure 4** Mean density (trees/ha) of seedlings for all 26 species combined per treatment per sampling year. Open bars: 2005; grey bars: 2007. The bars indicate 95% confidence intervals of the means. N = 7 replicates for the open access treatment (+E+N) and N = 12 for the partial (-E+N) and full exclusion (-E-N).



**Figure 5** Mean stem density (stems/ha) per height class (i.e. seedlings:  $\leq 0.5$ m; saplings: 0.51 – 1.5 m) for all 26 species combined per treatment. Open access (+E+N, open bars), partial exclusion (-E+N, diagonal hatching) and full exclusion (-E-N, grey bars). The bars indicate 95% confidence intervals of the means. N = 12 replicates per treatment.



**Figure 6** Size distribution curves of three common Sand Forest species in the three treatments: a, height class distribution (i.e. seedlings:  $\leq 0.5$ m, saplings; 0.51 – 1.5 m); b, linear regression of diameter class distribution. Open access (+E+N, open bars, grey circles and lines), partial exclusion (-E+N, diagonal hatching, red circles and lines) and full exclusion (-E-N, grey bars, black circles and lines). The bars (a) and dotted lines (b) indicate 95% confidence intervals. N = 12 replicates per treatment.



**Figure 7** Size distribution curves of three characteristic Sand Forest species in the three treatments: a, height class distribution (i.e. seedlings:  $\leq 0.5\text{m}$ ; saplings; 0.51 – 1.5m); b, linear regression of diameter class distribution. Open access (+E+N, open bars, grey circles and lines), partial enclosure (-E+N, diagonal hatching, red circles and lines) and full enclosure (-E-N, grey bars, black circles and lines). The bars (a) and dotted lines (b) indicate 95% confidence intervals. N = 12 replicates per treatment.

## Discussion

In addition to any effect small herbivores, rodents and invertebrates may have on recruitment (Shaw et al. 2002; Augustine and McNaughton 2004; Goheen et al. 2007), we show that forest regeneration is also impacted by both mega- and mesoherbivores as we managed to experimentally separate the browsing effects of elephant and nyala on recruitment. Both elephant and nyala potentially forage on recruiting individuals as the preferred feeding height of elephant falls between 1.0 and 2.0 m (Lagendijk 2003), and that of nyala between 0.6 and 1.1 m (Kirby et al. 2008).

Neither seedlings nor saplings of the three common and three characteristic focus species showed a significant effect from browsing. Elephants have been found to select for *D. schlechteri*, *N. hildebrandtii*, *P. myrtifolia* and *T. junodii*, and use *S. leptoclada* less selectively in Sand Forest in Tembe Elephant Park (TEP) (*U. caffra* does not occur in TEP; Matthews 2005). However, it may well be that elephant in Phinda do prefer the first four species, but do not impact on the seedlings or saplings. To our knowledge, feeding preferences of nyala have not yet been published. In addition, Sand Forest soil seed banks have been found to be poor in TEP (Kellerman and Van Rooyen 2007), which is consistent with the low seed bank densities for dry tropical forests (Kellerman and Van Rooyen 2007). Together with the short time frame of this study, this might explain the absence of a browsing effect on our focus species.

All three large tree species (*D. schlechteri*, *N. hildebrandtii* and *P. myrtifolia*) had size classes missing in the middle size cohorts, which may be explained by previous human utilisation of stems. In the last 25 years, the human population in the region (Moll 1980; Kyle 2004) has drastically increased with a concurrent intensification of the use of forest products, such as construction timber, fuel wood, wood for curios and medicinal plants (Lawes et al. 2004; Gaugris and Van Rooyen 2007). Missing size classes may also be a result of poor recruitment in the past; however there is little consensus over the potential causes underlying low recruitment rates in Sand Forest, which range from climatic factors (e.g. drought), periodic recruitment events, to browsing pressure (Matthews 2005; Midgley et al. 2005; Kellerman and Van Rooyen 2007).

Regeneration success, and hence recruitment of woody species into taller height classes, is dependent on a variety of factors. Seedling mortality is size-dependent, with the highest mortality occurring in the height class below 10 cm (Turner 1990). This implies that seedlings are most at risk during the establishment phase, when young trees are often most palatable (Fenner and

Thompson 2005). Therefore, seedlings may need to escape a “browsing trap” (held in a height class making them more vulnerable to browsers) (Bond and Archibald 2003) induced by small- and medium-size herbivores (Belsky 1984; Prins and Van der Jeugd 1993; Goheen et al. 2004), before being able to grow into the sapling phase. Our results support this as we found increased survival of individual trees and stems where both nyala and elephant were excluded, suggesting that browsing pressure may have been a limiting factor for Sand Forest recruitment in the past. This is strengthened by the relatively higher stem density in the full exclosure (-E-N). Trees within the seedling height which were browsed just prior the initiation of the experiment may have coppiced by 2007 after browsing release. This indicates a continued browsing pressure in the other treatments, and an inhibition of recruitment due to browsing. In addition, seedling densities had increased within the open access treatment (+E+N) and the full exclosure (-E-N) between the sampling years, but not in the partial exclosure (-E+N). This could be due to spatial heterogeneity in seed rain between treatments, but is more likely to be caused by increased browsing by nyala in absence of elephant (Lagendijk et al. 2011) suppressing recruitment in the partial exclosure (-E+N). This effect of nyala is supported by the higher seedling densities found in the full exclosure (-E-N) from which they are excluded, than in the open access treatment (+E+N) where they are present with elephant.

While our research was conducted in one single Sand Forest patch, and we should thus be cautious with the interpretation of our results, we do believe that the mechanisms described here are applicable to other Sand Forest patches and other forest systems. Woodland populations are believed to benefit from a release from browsing pressure by megaherbivores (Goheen et al. 2007; Biggs et al. 2008; Kerley et al. 2008). Our findings (cf. Prins and Van der Jeugd 1993; Moe et al. 2009) argue this viewpoint as we show that also the effects of mesoherbivores in combination with megaherbivores on forests dynamics cannot be ignored. This illustrates that while attention is often focussed on the individual herbivore species, the importance of browsing effects by multiple species on vegetation has often been neglected. Therefore effects of both mega- and mesoherbivores need to be taken into account when conserving woodlands and forests. This is especially important in the context of the ‘elephant problem’ (Owen-Smith et al. 2006), where conservation managers are concerned with the impacts of increasing elephant population densities on the environment, which may lead to the loss of tall trees and possibly to the conversion of woodland to grassland (Caughley 1976; Kerley et al. 2008). While elephants can alter the vertical structure of vegetation from top down by impacting on tall trees, we show that both mega- and mesoherbivores in combination and nyala on their own, also have a strong top

down effect on seedlings in forests (cf. Moe et al. (2009) as a comparison to riparian woodlands for impala only), thereby preventing recruitment into taller height classes.

While two years of exclusion from browsers is a short time scale to observe changes in overall tree population structures (e.g. of individual species or in the larger height classes), this experiment shows that by manipulating disturbance factors (e.g. herbivory), changes in recruitment can be demonstrated within a short time interval (cf. Augustine and McNaughton 2004; 3 years). The exclosures as presented in this study are being maintained for long-term monitoring to better understand the effects of herbivores on woody vegetation. Our results suggest that the traditional notion that recruitment of Sand Forest is uncommon (Midgley et al. 1995; Matthews 2005) might be a misconception. We show that recruitment is taking place, at least into the seedling phase, but that further recruitment into taller height classes is prevented by strong browsing pressure. Certainly, the importance of browsing, and especially of multiple browsers, needs to be carefully considered in management planning for conservation areas.

We emphasise here the need to consider all possible factors influencing tree communities, and not only the “obvious” or “political” ones. In the case of Sand Forest, while fencing elephants from the Sand Forest will provide a reduction in damage to larger trees (Grant et al. 2008; Shannon et al. 2008), it would be critical to also exclude mesoherbivores in order to promote seedling recruitment and thus long-term sustainability of the few remaining Sand Forest patches in Southern Africa.

Since tourism revenues are an important source of income for most parks, the creation of botanical reserves within the protected area can be a lucrative management strategy. This type of management approach could also be applicable to other natural systems.

### **Acknowledgements**

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## References

- Augustine DJ, McNaughton SJ (2004) Regulation of shrub dynamics by native browsing ungulates on East African rangeland. *J Appl Ecol* 41: 45-58.
- Belsky AJ (1984) Role of small browsing mammals in preventing woodland regeneration in the Serengeti National Park, Tanzania. *Afr J Ecol* 22: 271-279.
- Ben-Shahar R (1998) Changes in structure of savanna woodlands in northern Botswana following the impacts of elephants and fire. *Plant Ecol* 136: 189-194.
- Bergquist J, Örlander G, Nilsson U (1999) Deer browsing and slash removal affect field vegetation on south Swedish clearcuts. *For Ecol Manage* 115: 171-182.
- Biggs HC, Slotow R, Scholes RJ, Carruthers J, Van Aarde RJ et al. (2008) Towards integrated decision making for elephant management. In: Scholes RJ, Mennell KG, editors. *Elephant Management: A Scientific Assessment for South Africa* Johannesburg: Witwatersrand University Press. pp. 537–586.
- Bond WJ, Archibald S (2003) Confronting complexity: fire policy choices in South African savanna parks. *International Journal of Wildland Fire* 12: 381-389.
- Botes A, McGeoch MA, Van Rensburg BJ (2006) Elephant- and human-induced changes to dung beetle (Coleoptera: Scarabaeidae) assemblages in the Maputaland Centre of Endemism. *Biol Conserv* 130: 573-583.
- Burke A (1997) The impact of large herbivores on floral composition and vegetation structure in the Naukluft Mountains, Namibia. *Biodiv Conserv* 6: 1203-1217.
- Cadenasso ML, Pickett STA, Morin PJ (2002) Experimental test of the role of mammalian herbivores on old field succession; community structure and seedling survival. *Journal of the Torrey Botanical Society* 129: 228-237.
- Caughley G (1976) The elephant problem - an alternative hypothesis. *E Afr Wildl J* 14: 265-283.
- Clarke KR, Warwick RM (2001) *Change in marine communities: an approach to statistical analysis and interpretation*. Plymouth, UK: PRIMER-E.
- Condit R, Sukumar R, Hubbell SP, Foster RB (1998) Predicting population trends from size distributions: a direct test in a tropical tree community. *Am Nat* 152: 495–509.
- de Garine-Wichatitsky M, Fritz H, Gordon IJ, Illius AW (2004) Bush selection along foraging pathways by sympatric impala and greater kudu. *Oecologia* 141: 66-75.
- Druce HC, Pretorius K, Druce D, Slotow R (2006) The effect of mature elephant bull introductions on ranging patterns of resident bulls: Phinda Private Game Reserve, South Africa. *Koedoe* 49: 77-84.

- Druce HC, Pretorius K, Slotow R (2008) The response of an elephant population to conservation area expansion: Phinda Private Game Reserve, South Africa. *Biol Conserv* 141: 3127-3138.
- Dublin HT, Sinclair ARE, McGlade J (1990) Elephants and fire as causes of multiple states in the Serengeti-Mara woodlands. *J Anim Ecol* 59: 1147-1164.
- Eckhardt HC, van Wilgen BW, Biggs HC (2000) Trends in woody vegetation cover in the Kruger National Park, South Africa, between 1940 and 1998. *Afr J Ecol* 38: 108-115.
- Everard DA, Midgley JJ, Van Wyk GF (1995) Dynamics of some forests in Kwa Zulu-Natal, South Africa, based on ordinations and size-class distributions. *S Afr J Bot* 61: 283-292.
- Fenner M, Thompson K (2005) *The ecology of seeds*. Cambridge: Cambridge University Press. 250 p.
- Fritz H, Duncan P, Gordon IJ, Illius AW (2002) Megaherbivores influence trophic guilds structure in African ungulate communities. *Oecologia* 131: 620-625.
- Gadd ME (2002) The impact of elephants on the marula tree *Sclerocarya birrea*. *Afr J Ecol* 40: 328-336.
- Gaugris JY, Van Rooyen MW (2007) The structure and harvesting potential of the sand forest in Tshanini Game Reserve, South Africa. *South African Journal of Botany* 73: 611-622.
- Gaugris JY, Van Rooyen MW, Bothma JDP (2008) Growth rate of selected woody species in northern Maputaland, KwaZulu-Natal, South Africa. *South African J Bot* 74: 85-92.
- Goheen JR, Young TP, Keesing F, Palmer TM (2007) Consequences of herbivory by native ungulates for the reproduction of a savanna tree. *J Ecol* 95: 129-138.
- Goheen JR, Keesing F, Allan BF, Ogada D, Ostfeld RS (2004) Net effects of large mammals on *Acacia* seedling survival in an African savanna. *Ecology* 85: 1555-1561.
- Grant CC, Bengis R, Balfour D, Peel M, Davies-Mostert HT et al. (2008) Controlling the distribution of elephants. In: Scholes RJ, Mennell KG, editors. *Elephant Management: A Scientific Assessment for South Africa*. Johannesburg: Witwatersrand University Press. pp. 329-369.
- Hagenah N (2006) Among rodents and rhinos: interplay between small mammals and large herbivores in a South African savanna [PhD]. Wageningen: Wageningen University. 146 p.
- Hawthorne WD, Parren MPE (2000) How important are forest elephants to the survival of woody plant species in Upper Guinean forests. *J Trop Ecol* 16: 133-150.
- Jacobs OS, Biggs R (2002) The impact of the African elephant on marula trees in the Kruger National Park. *S Afr J Wildl Res* 32: 13-22.

- Kellerman MJS, Van Rooyen MW (2007) Seasonal variation in soil seed bank size and species composition of selected habitat types in Maputaland, South Africa. *Bothalia* 37: 249-258.
- Kerley GIH, Landman M, Kruger L, Owen-Smith N, Balfour D et al. (2008) Effects of elephants on ecosystems and biodiversity. In: Scholes RJ, Mennell, KG, editors. *Elephant Management: A Scientific Assessment for South Africa*. Johannesburg: Witwatersrand University Press. pp. 146-205.
- Kirby T, Shannon G, Page B, Slotow R (2008) The influence of sexual dimorphisms on the foraging behaviour of the nyala *Tragelaphus angasii*. *Acta Zoologica Sinica* 54: 561-568.
- Kirkwood D, Midgley JJ (1999) The floristics of Sand Forest in northern KwaZulu-Natal, South Africa. *Bothalia* 29: 293-304.
- Kyle R (2004) Resource use in the indigenous forests of Maputaland: are conservation strategies working? In: Lawes MJ, Eeley HAC, Shackleton CM, Geach BGS, editors. *Indigenous Forests and Woodlands in South Africa: Policy, People and Practice*. Scottsville: University of KwaZulu-Natal Press. pp. 713-736.
- Lagendijk DDG (2003) Mopane woodlands: a food source for elephants [MSc thesis]. Wageningen: Wageningen University. 57 p.
- Lagendijk G, Page BR, Slotow R (2011) Short-term effects of single species browsing release by different-sized herbivores on Sand Forest vegetation community. *South Africa Biotropica* DOI: 10.1111/j.1744-7429.2011.00776.x
- Lawes MJ, Obiri JAF, Eeley HAC (2004) The uses and value of indigenous forest resources in South Africa In: Lawes MJ, Eeley HAC, Shackleton CM, Geach BGS, editors. *Indigenous Forests and Woodlands in South Africa: Policy, People and Practice*. Scottsville: University of KwaZulu-Natal Press. pp. 227-234.
- Levick S, Rogers K (2008) Patch and species specific responses of savanna woody vegetation to browser exclusion. *Biol Conserv* 141: 489-498.
- Lykke AM (1998) Assessment of species composition change in savanna vegetation by means of woody plants' size class distributions and local information. *Biodiv Conserv* 7: 1261-1275.
- Matthews WS (2005) Contributions to the ecology of Maputaland, southern Africa, with emphasis on Sand Forest [PhD]. Pretoria: University of Pretoria. 254 p.
- Matthews WS, Van Wijk AE, Van Rooyen N, Botha GA (2001) Vegetation of Tembe Elephant Park, Maputaland, South Africa. *S Afr J Bot* 67: 573-594.

- Merrill EH, Beyer HL, Jones GP, McDaniel GW (2003) Deciduous woodland conservation under heavy deer browsing on Devils Tower National Monument, USA. *J Nat Conserv* 10: 221-232.
- Midgley JJ, Everard DA, Van Wyk G (1995) Relative lack of regeneration of shade-intolerant canopy species in some South African forests. *S Afr J Science* 91: 7-8.
- Moe SR, Rutina LP, Hytteborn H, Du Toit JT (2009) What controls woodland regeneration after elephants have killed the big trees? *J Appl Ecol* 46: 223-230.
- Moll EJ (1980) Terrestrial plant ecology. In: Bruton MN, Cooper KH, editors. *Studies on the ecology of Maputaland: Rhodes University & The Natal Branch of the Wildlife Society of Southern Africa*. pp. 52-68.
- Mucina L, Rutherford MC (2006) *The vegetation of South Africa, Lesotho and Swaziland*; Mucina L, Rutherford MC, editors. Pretoria: South African National Biodiversity Institute.
- Obiri JAF, Lawes MJ, Mukolwe M (2002) The dynamics and sustainable use of high-value tree species of the coastal Pondoland forests of the Eastern Cape Province, South Africa. *For Ecol Manage* 166: 131-148.
- Owen-Smith RN (1988) *Megaherbivores: the influence of very large body size on ecology*. Cambridge: Cambridge University Press: 369 p.
- Owen-Smith N, Kerley GIH, Page B, Slotow R, Van Aarde RJ (2006) A scientific perspective on the management of elephants in the Kruger National Park and elsewhere. *S Afr J Sc* 102: 389-394.
- Pickett STA, Cadenasso ML, Benning TL (2003) Biotic and abiotic variability as key determinants of savanna heterogeneity at multiple spatiotemporal scales. In: du Toit JT, Rogers KH, Biggs HC, editors. *The Kruger Experience: ecology and management of savanna heterogeneity*. Washington: Island Press. pp. 22-40.
- Prins HHT, van der Jeugd HP (1993) Herbivore Population Crashes and Woodland Structure in East Africa. *J Ecol* 81: 305-314.
- Repton M (2007) *Vegetation utilisation by elephants in the Mkuze and Phinda Game Reserves [MSc]*. Durban: University of KwaZulu-Natal.
- Riginos C, Young TP (2007) Positive and negative effects of grass, cattle, and wild herbivores on *Acacia* saplings in an East African savanna. *Oecologia* 153: 984-995.
- Shannon G, Druce DJ, Page BR, Eckhardt HC, Grant R et al. (2008) The utilization of large savanna trees by elephant in southern Kruger National Park. *J Trop Ecol* 24: 281-289.

- Shannon G, Matthews WS, Page BR, Parker GE, Smith RJ (2009) The affects of artificial water availability on large herbivore ranging patterns in savanna habitats: a new approach based on modelling elephant path distributions. *Diversity and Distributions* 15: 776-783.
- Shaw MT, Keesing F, Ostfeld RS (2002) Herbivory on *Acacia* seedlings in an East African savanna. *Oikos* 98: 385-392.
- Siebert F, Eckhardt HC (2008) The vegetation and floristics of the Nkhuhlu exclosures, Kruger National Park. *Koedoe* 50: 126-144.
- Siebert SJ, Fish L, Uiras MM, Izidine SA (2004) Grass assemblages and diversity of conservation areas on the coastal plain south of Maputo Bay, Mozambique. *Bothalia* 34: 61-71.
- Smallie JJ, O'Connor TG (2000) Elephant utilization of *Colophospermum mopane*: possible benefits of hedging. *Afr J Ecol* 38: 352-359.
- Turner IM (1990) Tree seedling growth and survival in a Malaysian rain forest. *Biotropica* 22: 146-154.
- Van Wyk GF, Everard DA, Midgley JJ, Gordon IG (1996) Classification and dynamics of a southern African subtropical coastal lowland forest. *S Afr J Bot* 62: 133-142.
- Walker BH, Stone L, Henderson L, Vernede M (1986) Size structure analysis of the dominant trees in a South African savanna. *S Afr J Bot* 52: 397-402.

**CHAPTER 5**

**Short-Term Effects of Single Species Browsing Release by Different-Sized  
Herbivores on Sand Forest Vegetation Community, South Africa**

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**Abstract**

Manipulations of herbivores in protected areas may have profound effects on ecosystems. We examine short-term effects on tree species assemblages and resource utilisation by a mesoherbivore and small-size herbivores (ungulates < 20 kg) in Sand Forest, after browsing release from a megaherbivore (elephant), or both a mega- and mesoherbivore (nyala), respectively. Effects were experimentally separated using replicated exclosures where all trees were counted, identified to species and browsing events recorded. Tree species assemblages were impacted by both elephant and nyala, and by each herbivore species individually. Tree turnover rates were higher where both herbivore species were present than in their combined absence. Diet was segregated among elephant, nyala and small-size herbivores. Both resource specificity and browsing pressure by nyala increased in absence of elephant; small-size herbivores increased resource specificity in absence of elephant, and increased browsing pressure in absence of both elephant and nyala. This implies interference competition with competitive release. The indirect effect of the manipulation of herbivore populations, through the removal of one or two herbivore species, caused a shift in tree species composition and diet of smaller-size herbivores. These indirect effects, especially on tree species composition, can become critical as they affect vegetation dynamics, biodiversity and ecosystem processes. Therefore, in order to conserve habitats and biodiversity across all trophic levels, conservation managers should consider the effects of (i) the full herbivore assemblage present, and (ii) any effects of altering the relative and absolute abundance of different herbivore species on other herbivore species and vegetation.

**Key words:** elephant; exclosure; interference competition; Licuáti forest; *Loxodonta africana*; nyala; *Tragelaphus angasii*; vegetation change;

## Introduction

The current status of conservation results in many mammal species co-existing at high densities within small protected areas (Chapin *et al.* 2000, Slotow *et al.* 2005). Different-size herbivores can substantially impact conservation areas, and its ecological functioning, through their use of different food resources (Levick *et al.* 2009). Complex interactions between mechanisms such as predation, competition and facilitation promote co-existence of animal species (Pace *et al.* 1999), but disrupting these has functional consequences such as the modification of ecosystem processes (Hooper & Vitousek 1997, Tilman *et al.* 1997). When the density of a particular herbivore species is reduced, competitive release occurs, as the constraint of the competing herbivore species is removed (Kareiva 1982). The ‘released’ herbivore species now uses different food resources compared to when the competitor was present. The effect of this competitive release can cascade into lower trophic levels as the plant species composition shifts, in response to changed foraging behaviour of the released herbivore species, which ultimately affects ecosystem processes (Chapin *et al.* 2000).

The effects of competitive release of herbivores on vegetation have been studied extensively for groups of similar-size herbivores through exclusion experiments (Young *et al.* 1998, Shaw *et al.* 2002, Goheen *et al.* 2004, 2007, Levick & Rogers 2008, Moe *et al.* 2009). However, the effects of the selective removal of one or two key herbivores on resource utilisation by smaller herbivores, and the effects of the consequent browsing release by a single herbivore species on tree communities, are less well known (Schmitz *et al.* 2000). Understanding the effects of browsing release is especially important in protected areas subject to active herbivore management (*e.g.* population reductions, removal or introduction).

African ungulates provide a unique opportunity to test for such within-guild effects because of their diversity (Du Toit & Cumming 1999), different functional groups (Prins & Douglas-Hamilton 1990), abundance, and active conservation management (*e.g.* Carruthers *et al.* 2008, Morgan *et al.* 2009). Here we distinguish among mega- (species with a body mass  $\geq 1000$  kg (Owen-Smith 1988)), meso- (medium-size herbivores 50 to 450 kg (Fritz *et al.* 2002, de Garine-Wichatitsky *et al.* 2004)) and small-size herbivores (ungulates  $< 20$  kg (Bothma *et al.* 2004)).

We focus on Sand Forest, a deciduous dry forest endemic to north-eastern South Africa and southern Mozambique (Kirkwood & Midgley 1999, Matthews *et al.* 2001, Siebert *et al.* 2004). In the two main localities where Sand Forest is conserved in South Africa, both elephant *Loxodonta*

*africana*, a megaherbivore (♀: 2500 kg; ♂: 5000 kg (Owen-Smith 1988)), and nyala *Tragelaphus angasii*, a mesoherbivore (♀: 65 kg; ♂: 110 kg (Kirby *et al.* 2008)), became locally abundant after fencing the protected area (*i.e.* Tembe Elephant Park), and reintroduction (*i.e.* Phinda Private Game Reserve). Although few large mammal species utilise Sand Forest (Matthews 2005), both elephant and nyala do, and impact on the structural diversity while foraging (Matthews 2005, Kirby *et al.* 2008). In addition, it is expected that each herbivore species also affects tree species composition. The browsing herbivore community within Sand Forest also includes small-size herbivores, such as common duiker *Sylvicapra grimmia*, red duiker *Cephalophus natalensis*, and suni *Neotragus moschatus*. The Sand Forest ecosystem thus provides a relatively simplified large herbivore browsing guild in terms of diversity, while being complete in terms of complexity, including the full spectrum of different-size herbivores (*i.e.* mega-, meso- and small-size herbivores).

By excluding either a megaherbivore, or both mega- and mesoherbivores, using a replicated enclosure experiment, we created the opportunity to study competitive release when key elements (*i.e.* elephant and/or nyala) were artificially removed. While testing for these effects, we focused firstly on changes in woody vegetation communities, expecting the removal of a key herbivore species, with consequential browsing release for other herbivores, to alter tree species assemblages. Secondly, we focused on dietary segregation between different herbivore groups, expecting diet overlap and browsing pressure of nyala and small-size herbivores to increase due to browsing release after exclusion of their larger counterparts. Resource availability for small-size herbivores should be greater within their height reach due to browsing release by nyala (Lagendijk *et al.* 2011) as they feed in overlapping height ranges, and potential competitive displacement by larger herbivores (*i.e.* elephant and/or nyala) is eliminated when these animals are removed.

Therefore, the objectives were to determine the short-term effects of browsing release, on (1) tree species assemblages, and (2) resource utilisation by a mesoherbivore and small-size herbivores after browsing release by their larger counterparts, *i.e.* (i) a megaherbivore (elephant) or (ii) both a mega- and mesoherbivore (elephant and nyala).

To our knowledge this is the first study to experimentally separate the effects of one mega- and mesoherbivore on tree species assemblages, and resource utilisation by smaller-size ungulate herbivores. This in contrast to other experimental studies, which excluded groups of similar-size

herbivores, with observed effects not ascribed to one particular herbivore species. It is imperative to recognise single species effects as these may be confounded in multi-species assemblages. As conservation managers manipulate at a single species level, understanding the ecological role, or the effect of removing it, of each individual species is crucial.

## Methods

### *Study area*

This study was conducted in the endemic Sand Forest in Phinda Private Game Reserve (Phinda 27°92' - 27°68' S; 32°44' - 32°20' E), a 180 km<sup>2</sup> conservation area in Maputaland, northern KwaZulu-Natal, South Africa. A wide range of other habitat types are present in the reserve, including western Maputaland sandy bushveld (Mucina and Rutherford 2006). The climate is subtropical with hot, humid summers (November – April) and warm, dry winters (May – October). Temperatures range from 10°C in winter to 35°C in summer. Annual rainfall varies spatially from west to east between 350 mm and 1100 mm.

Phinda was created in 1991, after which game was introduced. Fifty-eight elephant were released between 1992 and 1994 (Druce *et al.* 2006). At the start of this study (2005), 75 elephant were present, which increased to 98 individuals in 2007 (based on an individually identified and monitored elephant population (*e.g.* Druce *et al.* 2008)). Nyala numbered approximately 1100 and 1750 individuals in 2005 and 2007, respectively (based on annual aerial game counts). Other browsing ungulates on Phinda include giraffe *Giraffa camelopardalis* (2007 annual helicopter game count 154), kudu *Tragelaphus strepsiceros* (188), impala *Aepyceros melampus* (1690), red duiker (23), common duiker (no count available) and suni (no count available). The only mega- and mesoherbivore utilising the Sand Forest patches in Phinda were elephant and nyala; giraffe, kudu, and impala did not use the forest (D. D. G. Lagendijk, pers. obs.).

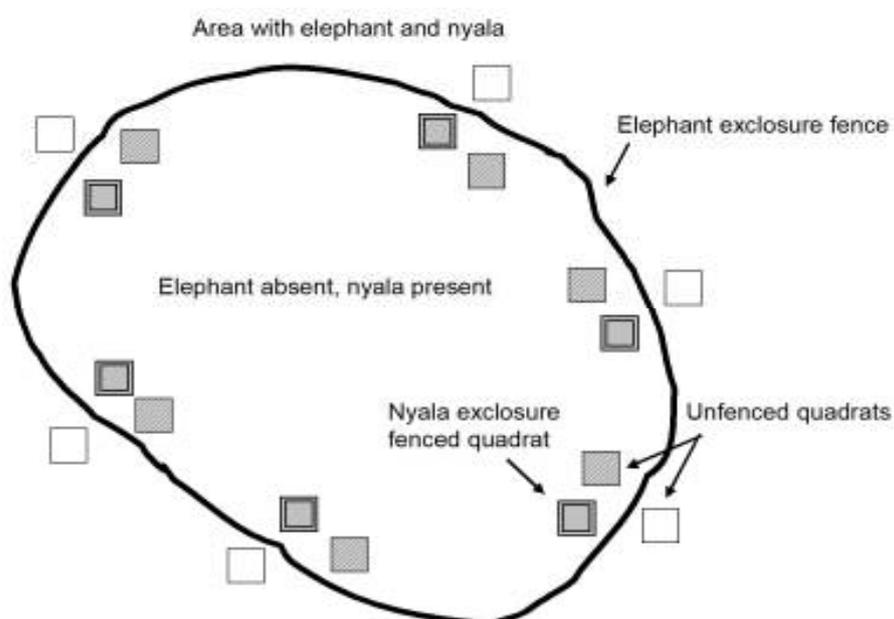
Sand Forest is a dense vegetation type, with a closed canopy 5 to 12 m in height and without a significant understorey, growing on acidic, sandy soils with very little clay (Matthews *et al.* 2001). Characteristic tree species include *Balanites maughamii*, *Cleistanthus schlechteri*, *Cola greenwayi*, *Croton pseudopulchellus*, *Dialium schlechteri*, *Drypetes arguta*, *Hymenocardia ulmoides*, *Newtonia hildebrandtii*, *Pteleopsis myrtifolia*, *Strychnos henningsii* and *Toddaliopsis bremekampii* (Moll 1980, Kirkwood & Midgley 1999, Matthews 2005).

*Experimental set-up*

In November 2005, part of the Sand Forest was fenced from elephants using electrified strand wires as part of a long-term (> 10 yr) vegetation monitoring experiment (Fig. 1). The fence consisted of two electrified (60 pulses of 7000 V/min) high tension galvanized wires (2.4 mm thick), approximately 1.8 m and 2 m above the ground, enclosing 3.09 km<sup>2</sup> of a 5.2 km<sup>2</sup> Sand Forest patch. For logistical reasons the fence mainly followed existing roads and did not follow the shape of the Sand Forest edge. To exclude nyala within this area, 20 x 20 m enclosures were erected, using 1.8 m high bonnox fencing (a coarse wire mesh with 30 x 20 cm openings). The 'gaps' in this fencing allow passage for small-size herbivores such as duiker and suni. The resulting experimental design consisted of a set of three 400 m<sup>2</sup> treatments in close proximity: (1) unfenced area available to all herbivores (full access); (2) area fenced to exclude only elephant (partial enclosure); (3) area fenced to exclude nyala and elephant (full enclosure), but providing access to duiker and suni. There were 12 replicates (*i.e.* sites) of this set of three treatments. Distances between sites ranged from 0.12 to 2.75 km, and the distance of each set from the edge of the Sand Forest patch varied (range: 130 - 280 m). Both elephant and nyala were utilising this Sand Forest patch prior to the time the enclosure fences went up (Kirby *et al.* 2008, T. Dickerson, pers. comm.), at which time the browsing effect of these herbivores was removed from the respective areas.

In 2005, a base-line survey was conducted, which was followed-up in 2007, allowing us to determine short-term effects. Teams of 4 - 8 people worked systematically through each 20 x 20 m plot, counting and identifying all woody individuals (*i.e.* including seedlings; > 0.02 m and ≤ 0.5 m tall). In addition, each woody individual was carefully examined, and utilisation was ascribed to elephant, nyala or small-size herbivores based on adaptations of the methods of Walker (1976), Wiseman *et al.* (2004) and Makhabu *et al.* (2006b). Leaf stripping and branch removal by even very small elephants is easily detected as well as single bites by nyala and the small-size herbivores. The presence of spoor, plant part used, height of removal, biomass removed, sharpness of the bite (ungulate) or break (elephant) were used as indicators of which herbivore species had utilised the woody individual.

Five full access plots were repositioned in 2007, therefore when doing pairwise across year comparisons with the other treatments only 7 full access treatments were included in the analyses.



**Figure 1** A schematic representation of the experimental design of the enclosure experiment with three treatments: (1) full access, accessible for all herbivores (open squares); (2) partial enclosure, elephant excluded, nyala present (diagonal hatching); (3) full enclosure, both elephant and nyala excluded (grey squares). The sets of three treatments were replicated 12 times (only six times shown in schematic).

#### *Data-analyses*

Following recommendations by Clarke and Warwick (2001), tree species contributing less than 4 percent of the abundance per plot in 2005 were discarded. Consequently a total of 27 tree species were included in all analyses, unless stated otherwise (Appendix S5.1).

Tree densities were scaled up from 400 m<sup>2</sup> to 1 ha. For the 27 species, in 2005 differences in tree density and tree species richness among treatments were non significant ( $F_{2,33} = 0.809$ ,  $P = 0.454$  and  $F_{2,33} = 2.432$ ,  $P = 0.103$ , respectively); therefore replicates were considered to be initially homogeneous (Table 1, Lagendijk *et al.* 2011). By 2007, tree densities were significantly different among treatments ( $F_{2,33} = 5.180$ ,  $P = 0.011$ ), with significantly greater densities in the full enclosure than in the full access treatment (Tukey:  $P = 0.010$ ) (Table 1, Lagendijk *et al.* 2011). Tree densities in the partial enclosure did not significantly differ from the full access and the full enclosure treatments. In 2007, species richness was still not significantly different among treatments ( $F_{2,33} = 1.183$ ,  $P = 0.319$ ) (Table 1, Lagendijk *et al.* 2011).

**Table 1** The short-term effects of browsing release, by means of herbivore exclusion, on tree densities and species richness (mean  $\pm$  SE) in Sand Forest (see Lagendijk et al. 2011 for full analysis).

	Year	Treatment		
		Full access <sup>a</sup>	Partial enclosure <sup>b</sup>	Full enclosure <sup>c</sup>
Densities (trees/ha)	2005	7227 $\pm$ 634	8158 $\pm$ 929	8710 $\pm$ 887
	2007	8283 $\pm$ 988	9938 $\pm$ 1075	14269 $\pm$ 1862
Species richness	2005	18.8 $\pm$ 0.88	16.7 $\pm$ 0.68	16.7 $\pm$ 0.74
	2007	16 $\pm$ 0.74	15 $\pm$ 1.51	17.8 $\pm$ 0.82

<sup>a</sup> Unfenced area accessible for all herbivores; <sup>b</sup> Area fenced to exclude elephant; <sup>c</sup> Area fenced to exclude nyala and elephant, but accessible to small-size herbivores (*i.e.* duiker and suni)

To determine the effect of browsing release on vegetation, tree species assemblages (which includes both tree species composition and abundances) were compared per treatment between sampling years, and among treatments within 2005 and 2007, by comparing the species-abundance matrices.

We used a *PRO*crustean randomisation *TEST* (*PROTEST*) (Jackson 1995), by which two tree species assemblage matrices are compared, with a rotational-fit algorithm minimising the sum-of-squared residuals ( $m^2$ ) between the two matrices. The  $m^2$  statistic, a goodness-of-fit measure, ranges from 0 to 1, with a lower value indicating a higher similarity between two assemblages (King & Jackson 1999). Following Jackson (1995), a low *P*-value (based on a randomisation procedure) indicates a significant concordance, *i.e.* the concordant pattern is not due to chance. The program ran in *PROTEST* (Jackson 1995) using 9,999 random permutations. *PROTEST* has a stronger statistical power than the more conventionally used Mantel test (Peres-Neto & Jackson 2001).

Relative changes in abundances were calculated per tree species per site within each treatment between the two sampling years following Olofsson *et al.* (2004):

$$Rca_i = \ln\left(\frac{X_{i2007}}{X_{i2005}}\right)$$

where  $Rca_i$  is the relative change in abundance of tree species  $i$ ,  $X_{i2007}$  is the abundance for tree species  $i$  in 2007, and likewise  $X_{i2005}$  for 2005. Data were 'x + 1' transformed before calculation of  $Rca_i$ . We used Kruskal-Wallis to test these  $Rca_i$  values for differences among treatments.

Change in tree species over time was calculated per site per treatment in a pairwise comparison between years. Beta-diversity indices are more conventionally used to elucidate spatial species turnover, but here we used them to quantify temporal turnover. We used Cody's measure of beta-diversity ( $\beta_{co}$ ), which allows us to explore compositional differences in tree species assemblage, particularly tree species gain and losses, as opposed to differences in tree species richness, such as Whittaker's beta diversity index (Koleff *et al.* 2003). After re-expression by Koleff *et al.* (2003) and Cardoso *et al.* (2009),  $\beta_{co}$  can be described as follows:

$$\beta_{co} = 1 - \frac{a(2a + b + c)}{2(a + b)(a + c)}$$

where  $a$  is the number of tree species present in both sampling years,  $b$  the gain of tree species in 2007 and  $c$  the number of tree species lost since 2005.  $\beta_{co}$  ranges from 0 to 1 (low to high tree species turnover). Differences in turnover between the sampling years among treatments were tested using ANOVA, with treatment as fixed effect.

All tree species monitored in 2007 ( $n = 143$ ) were included in the analyses testing for competitive release by nyala and/or elephant on resource utilisation (*i.e.* diet diversity, diet breadth, resource specificity, diet overlap and browsing pressure). While the small-size herbivore group includes three possible species (*i.e.* red duiker, common duiker and suni), we here treat these three herbivores as a single group in the analyses, as they feed on a wide range of food items with only little specialisation (Prins *et al.* 2006).

Diet diversity was calculated as the number of tree species utilised per herbivore group per treatment. Differences in diet diversity among treatment and herbivore groups were tested using ANOVA, with treatment and herbivore group as fixed effects, after  $\log_{10}$ -transformation to attain normality of data.

Diet breadth  $B$ , which represents diet diversity (diet segregation), was calculated per herbivore group as niche breadth, following Levins (1968):

$$B = \frac{1}{\sum p_i^2}$$

where  $p_i$  is the proportion of all browsing events on tree species  $i$  in the diet. Differences in diet breadth among herbivore groups were tested using ANOVA, with herbivore group as fixed effect.

Resource specificity, or diet exclusivity, was calculated as the number of tree species used by one particular herbivore group relative to the number of species utilised by all herbivores in the experiment or particular treatment. Differences among treatment and herbivore groups were tested using ANOVA, with treatment and herbivore group as fixed effects.

Diet overlap  $O_{jk}$  between the different herbivore groups  $j$  and  $k$  was calculated for the full access and partial enclosure treatment, using Pianka's index for niche overlap (Pianka 1973):

$$O_{jk} = \frac{\sum (p_{ij} \cdot p_{ik})}{\sqrt{\sum p_{ij}^2 \cdot \sum p_{ik}^2}}$$

Where  $p_{ij}$  and  $p_{ik}$  are the proportions of tree species  $i$  within the 0.5-2.0 m height class, utilised by the  $j^{\text{th}}$  and the  $k^{\text{th}}$  herbivore group respectively. Diet overlap ranges from 0 (no tree species common in diets between herbivore groups  $j$  and  $k$ ) to 1 (identical tree species have been utilised by both groups in equal proportions). Pianka indices were calculated using EcoSim 7.0 (Gotelli & Entsminger 2004). Differences in diet overlap among the three herbivore groups in the full access treatment were analysed using Kruskal-Wallis, and differences in diet overlap between nyala and small-size herbivores between the full access and the partial enclosure treatment were analysed using ANOVA with herbivore group as fixed effect, after square-root transformation to attain normality of data.

Browsing pressure was calculated as the density of trees impacted by elephant, nyala or small-size herbivores proportional to tree availability (trees/ha). Differences in browsing pressure were tested among treatment per herbivore group using ANOVA, with treatment and site as fixed effects.

'Site' has only been included in the ANOVA model when it is a significant factor (2-tailed P-value). In all other instances it has been removed from the model to increase statistical power for testing the treatment and herbivore group effects. Where applicable, all significant ANOVAs ( $P < 0.05$ ) were followed-up with Tukey's *post-hoc* test. ANOVAs and Kruskal-Wallis analyses were performed using SPSS 15.0 (SPSS Inc., Chicago, U.S.A.).

## Results

Most interestingly, the PROTEST results showed no change in tree species assemblage within the full enclosure ( $P = 0.0006$ ; note that  $P < 0.05$  indicates no significant change in this case) since

the initiation of the experiment in 2005 to the resurvey in 2007 (Table 2; Fig. 2). This was in contrast to significant changes between 2005 and 2007 in assemblages where all herbivores were present (full access,  $P = 0.052$ ), and, more strongly, where only elephant were excluded (partial enclosure,  $P = 0.587$ ). Consistent with this, when contrasting among treatments in 2007, the tree species composition in the full enclosure (excluding both elephant and nyala, but allowing small-size herbivores) differed significantly from both other treatments (full access vs. full enclosure,  $P = 0.626$ ; partial vs. full enclosure,  $P = 0.508$ ). The change in assemblages from 2005 to 2007 within the full access and within the partial enclosure, was convergent across the two treatments, as the tree species assemblages between these two treatments were concordant ( $P = 0.0014$ ) in 2007. Thus, the full complement of herbivores, or excluding only elephant, resulted in a shift from 2005 to 2007 towards a similar tree species assemblage in 2007 (Table 2; Fig. 2). In contrast, a release of direct browsing pressure by both elephant and nyala, but with herbivory by small-size herbivores, did not affect tree communities over this time scale (Table 2; Fig. 2). While the direct treatment contrast within 2007 indicated no effect of excluding elephant (full and partial access assemblages not significantly different) (Table 2; Fig. 2), their starting assemblages in 2005 were different, confounding this contrast (as opposed to density and richness, see methods). Similarly, the significant effect, within 2007, of excluding both elephant and nyala (full access significantly different from full enclosure (Table 2; Fig. 2)), needs to be interpreted with caution because of different starting assemblages in 2005, and because there was no statistical significant change in assemblages from 2005 to 2007 within the full enclosure.

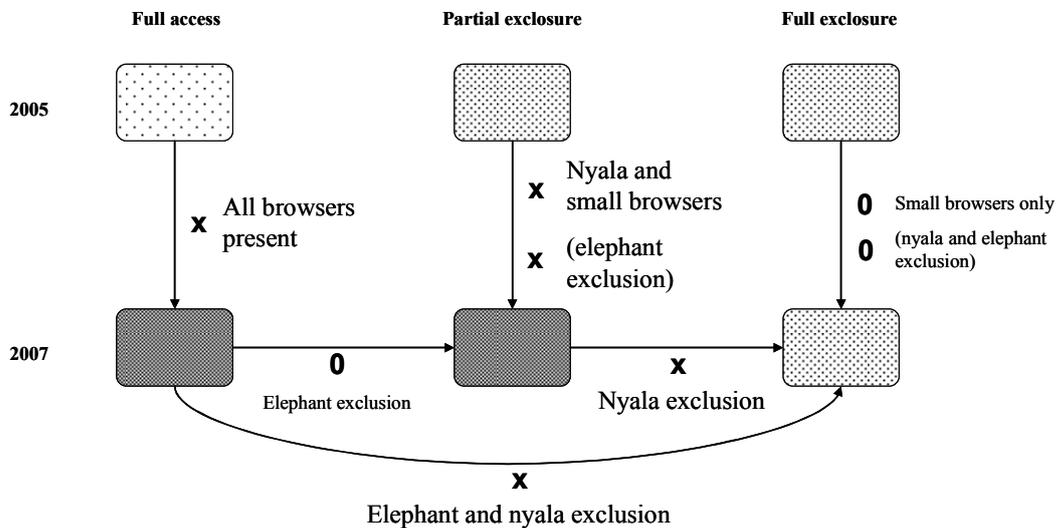
Overall, relative changes in abundances differed significantly among treatments ( $\chi^2_2 = 30.806$ ,  $P < 0.0005$ ), with significantly larger relative changes in abundances in the full access treatment than in either the partial ( $\chi^2_2 = 6.516$ ,  $P = 0.011$ ) or the full enclosure ( $\chi^2_2 = 28.121$ ,  $P < 0.0005$ ), and with significantly smaller changes in the full enclosure than in the partial enclosure ( $\chi^2_2 = 12.304$ ,  $P < 0.0005$ ). Thus, there was a negative effect of the full complement of herbivores, and nyala, respectively, on tree species abundances. In each treatment, the relative change in abundance was tree species specific (full access:  $\chi^2_{26} = 43.505$ ,  $P = 0.017$ ; partial enclosure:  $\chi^2_{26} = 46.075$ ,  $P = 0.009$ ; full enclosure:  $\chi^2_{26} = 76.660$ ,  $P < 0.0005$ ; Appendix S5.2). To identify the tree species responsible for this effect, however, required 27 Kruskal-Wallis tests, which necessitates the critical alpha to be Bonferroni-adjusted to 0.001 to avoid compounding Type 1 errors; this resulted in none of the tree species being statistically significantly different. The strongest changes occurred in the decline of *Sideroxylon inerme* in full access and *Zanthoxylon* sp. in the partial enclosure (Appendix S5.2).

**Table 2** The short-term effects of browsing release, by means of herbivore exclusion, on tree species assemblages in Sand Forest. *PRO*crustean randomisation *TEST* (*PROTEST*) results of comparisons of tree species assemblages between sampling years (2005 and 2007) per treatment, and pairwise treatment comparisons per sampling year<sup>a</sup>. All pairwise comparisons include data from 12 replicates with the exception of the comparison between tree species assemblages in the full access treatment between 2005 and 2007, which only incorporates 7 replicates.

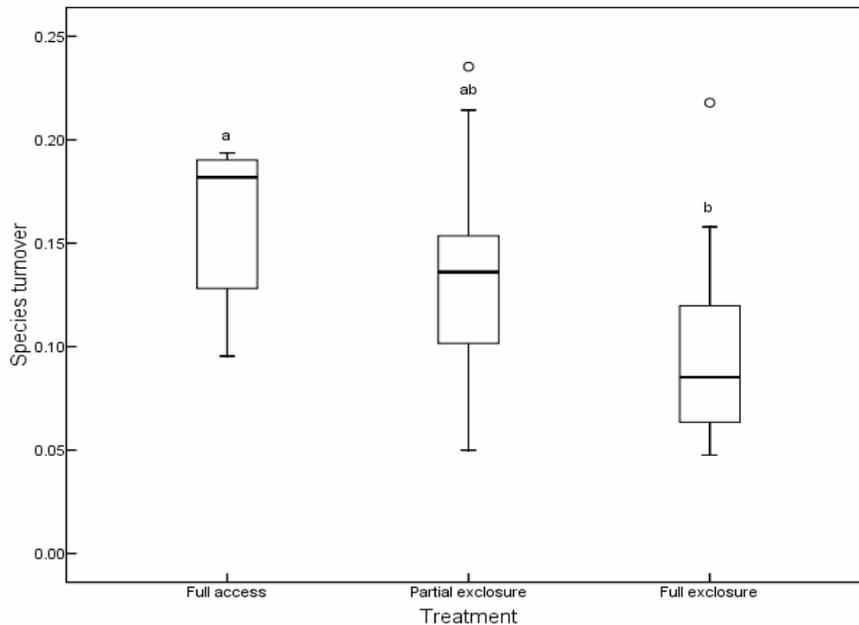
	Full access <sup>b</sup>	Partial enclosure <sup>c</sup>	Full enclosure <sup>d</sup>
2005 vs. 2007	$m^2 = 0.323$ $P = 0.052^a$	$m^2 = 0.643$ $P = 0.587^a$	$m^2 = 0.342$ $P = 0.0006$
	Full access vs. Partial enclosure	Partial enclosure vs. Full enclosure	Full access vs. Full enclosure
2005	$m^2 = 0.547$ $P = 0.094^a$	$m^2 = 0.457$ $P = 0.008$	$m^2 = 0.682$ $P = 0.538^a$
2007	$m^2 = 0.376$ $P = 0.001$	$m^2 = 0.604$ $P = 0.508^a$	$m^2 = 0.703$ $P = 0.626^a$

<sup>a</sup> Significant biological changes are presented in bold (note that  $P < 0.05$  indicates no significant change in this case)

<sup>b</sup> Unfenced area accessible for all herbivores; <sup>c</sup> Area fenced to exclude elephant; <sup>d</sup> Area fenced to exclude nyala and elephant, but accessible to small-size herbivores (*i.e.* duiker and suni)



**Figure 2** A schematic representation of the short-term effects of different herbivore groups on tree species assemblages in Sand Forest derived from the *PRO*crustean randomisation *TEST* (*PROTEST*) results (boxes with identical patterns represent similar tree species assemblages; 0: no significant effect on assemblages; X: significant effect on assemblages).



**Figure 3** The short-term effects of herbivore release on tree species turnover ( $\beta_{co}$ ) between 2005 and 2007 per treatment in Sand Forest.  $\beta_{co}$  ranges from 0 to 1 (low to high species turnover). Full access, accessible for all herbivores; partial enclosure, elephant excluded, nyala present; full enclosure, both elephant and nyala excluded. Data are range (whiskers), 25 and 75 % quartiles (box), and median (line).  $N = 7$  replicates for the full access treatment and  $N = 12$  for both the partial and full enclosure. Different letters indicate significant differences in tree species turnover among treatments ( $P < 0.05$ ).

Tree species turnover (beta-diversity over time) changed significantly between the sampling years among treatments ( $F_{2,28} = 3.416$ ,  $P = 0.047$ ; Fig. 3; Appendix S5.3). Turnover rates were significantly lower in the full enclosure than in the full access treatment (Tukey: 0.048). This indicates that the presence of both elephant and nyala increased tree species compositional change more than browsing by only small-size herbivores.

In total, 74 out of 143 tree species were browsed by all of the herbivores in the 2007 survey. Overall, small-size herbivores fed on the widest range of food sources ( $n = 61$ ) compared to nyala ( $n = 40$ ) or elephant ( $n = 30$ ). The  $\log_{10}$ -transformed number of tree species browsed was significantly different among treatment ( $F_{2,65} = 2.811$ ,  $P(1\text{-tailed}) = 0.034$ ), being significantly higher in the full enclosure than in the full access treatment (Tukey:  $P(1\text{-tailed}) = 0.012$ ). However, there was no significant effect among herbivore groups ( $P(1\text{-tailed}) = 0.129$ ), nor an interaction effect between herbivore group and treatment ( $P(1\text{-tailed}) = 0.452$ ; Table 3; Appendix S5.3).

**Table 3** The effect of competitive (browsing) release on resource utilisation for three groups of herbivores.<sup>a</sup> See text for statistical significant results.

	Full access <sup>b</sup>	Partial enclosure <sup>c</sup>	Full enclosure <sup>d</sup>
<i>Total number of tree species browsed</i>			
Elephant	30 (6.5, 0.44)	-	-
Nyala	27 (4.8, 0.57)	32 (6.3, 0.62)	-
Small-size herbivores	32 (6.1, 0.65)	30 (7.1, 0.25)	51 (11.0, 0.84)
<i>Diet breadth<sup>e</sup></i>			
Elephant	3.3, 0.47	-	-
Nyala	2.5, 0.47	3.1, 0.64	-
Small-size herbivores	2.8, 0.46	2.6, 0.28	4.0, 0.62
<i>Resource specificity<sup>f</sup></i>			
Elephant	21 %	-	-
Nyala	8 %	32 %	-
Small-size herbivores	21 %	27 %	100 %
<i>Mean dietary overlap (<math>\bar{O}</math>)<sup>g</sup></i>			
Elephant vs. small-size herbivores	0.04 (range 0 - 0.15)	-	-
Elephant vs. nyala	0.11 (range 0 - 1)	-	-
Nyala vs. small-size herbivores	0.15 (range 0 - 0.58)	0.26 (range 0 - 1)	-

<sup>a</sup> The number of tree species browsed (mean, CV), diet breadth (mean, CV), exclusive diet use, and mean diet overlap

<sup>b</sup> Unfenced area accessible for all herbivores; <sup>c</sup> Area fenced to exclude elephant; <sup>d</sup> Area fenced to exclude nyala and elephant, but accessible to small-size herbivores (*i.e.* duiker and suni); <sup>e</sup> Mean diversity of diet, measured as diet (niche) breadth; <sup>f</sup> Percentage of tree species exclusively used by herbivore group; <sup>g</sup> Mean proportion of overlap in utilised tree species among herbivore groups ( $N = 12$  replicates), ranging from 0 (no forage species in common) to 1 (full overlap in forage species).

Dietary breadth did not differ significantly among herbivore groups ( $F_{2,68} = 0.445$ ,  $P(1\text{-tailed}) = 0.322$ ; Table 3; Appendix S5.3).

Both nyala and small-size herbivores increased their exclusive use of tree species (resource specificity) when their larger counterparts were absent ( $F_{1,22} = 5.338$ ,  $P = 0.031$  and  $F_{1,22} = 6.699$ ,  $P = 0.017$  respectively; Table 3; Appendix S5.3). In the partial enclosure without elephant, nyala demonstrated a significantly higher resource specificity ( $F_{1,22} = 5.234$ ,  $P = 0.032$ ; Table 3; Appendix S5.3) than did small-size herbivores. In the full access treatment, both elephant and

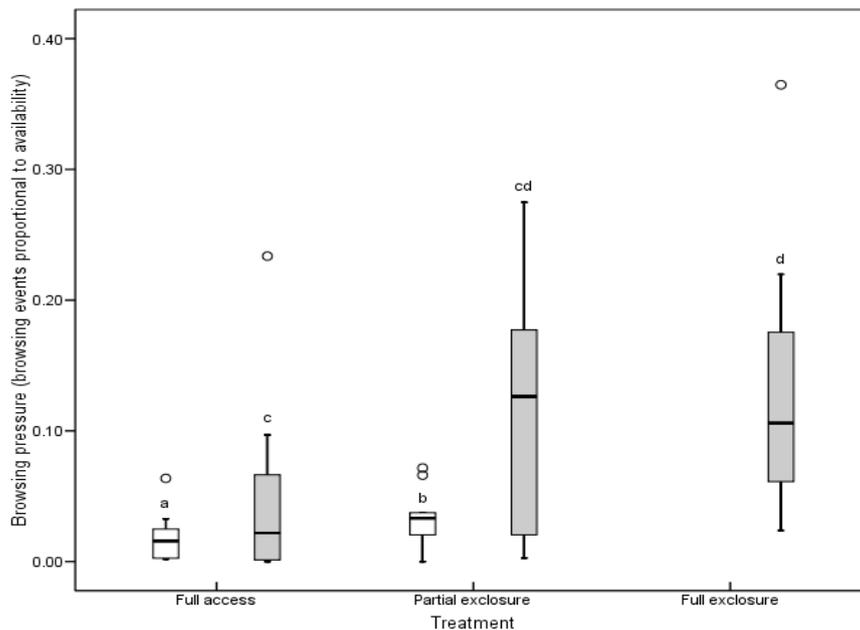
small-size herbivores exclusively used 21 percent of tree species, while nyala used only 8 percent of the tree species exclusively (marginally not significant ( $F_{2,32} = 3.164$ ,  $P = 0.056$ ; Table 3; Appendix S5.3)).

Diet overlap between all herbivore groups was low (elephant vs. small-size herbivores ( $\bar{O} = 0.04$ ), elephant vs. nyala ( $\bar{O} = 0.11$ ) and nyala vs. small-size herbivores ( $\bar{O} = 0.15$ )), and was not significantly different ( $\chi^2_2 = 1.451$ ,  $P = 0.484$ ) in the full access treatment, where all herbivore species were present (Table 3). Diet overlap between nyala and small-size herbivores was not significantly higher in the partial enclosure ( $\bar{O} = 0.26$ ) relative to the full access treatment ( $\bar{O} = 0.15$ ) (square-root transformed:  $F_{1,22} = 0.146$ ,  $P = 0.706$ ; Table 3; Appendix S5.3).

Browsing pressure (*i.e.* browsing events proportional to availability) by small-size herbivores differed significantly among treatments ( $F_{2,22} = 4.716$ ,  $P(1\text{-tailed}) = 0.010$ ) and site ( $F_{2,11} = 2.819$ ,  $P = 0.019$ ; Fig. 4; Appendix S5.3), with significantly more browsing events in the full enclosure than in the full access treatment (Tukey:  $P(1\text{-tailed}) = 0.012$ ). This indicates that small-size herbivores preferred browsing in the absence of both elephant and nyala, or had more resources available within their reach. Nyala browsing events were significantly more frequent in the partial enclosure than in the full access treatment ( $F_{1,22} = 3.621$ ,  $P(1\text{-tailed}) = 0.035$ ; Fig. 4; Appendix S5.3), indicating an increase in browsing pressure in the absence of elephant.

## Discussion

Active management in protected areas has become more widespread (*e.g.* Du Toit 1995, Bond & Loffell 2001, Slotow *et al.* 2005, Gusset *et al.* 2008, Trinkel *et al.* 2008), but the direct effects on other guild members, and the indirect effects for lower trophic levels are poorly known. We demonstrated the short-term effects of browsing release of a mega- and mesoherbivore on tree species assemblages and resource utilisation by smaller-size herbivores (*i.e.* nyala and small-size herbivores such as duiker and suni), through the artificial removal of one or two key herbivore species. A number of other enclosure studies in different habitats have also shown a shift in vegetation composition after excluding groups of similar-size herbivores for both the short-term (Jachmann & Croes 1991, Gill 2001, Augustine & McNaughton 2004) and long-term (Smart *et al.* 1985, Bakker *et al.* 2006, Guldmond & Van Aarde 2007, Levick & Rogers 2008), but not browsing release effects from the removal of a single herbivore species. The effects of single



**Figure 4** The short-term effects of herbivore release on browsing pressure by nyala (open bars) and small-size herbivores (grey bars) per treatment in Sand Forest. Full access, accessible for all herbivores; partial exclosure, elephant excluded, nyala present; full exclosure, both elephant and nyala excluded. Data are range (whiskers), 25 and 75 % quartiles (box), and median (line).  $N = 12$  for each treatment. Different letters indicate significant differences in browsing pressure by nyala ('a, b') and small-size herbivores ('c, d') among treatments ( $P < 0.05$ ).

species may be obscured by other similar-size herbivores in multi species assemblages. Effects may be wrongfully attributed to other species, which may lead to inappropriate management.

It would be expected that when tree densities are higher, interspecific competition among trees will start to play a greater role, and increase turnover rates. However, the full exclosure (small-size herbivores only) had a higher tree density, but lower turnover rates. This indicates that turnover rates here are more likely to be affected by herbivory than by interspecific competition among trees (Bond *et al.* 2001), which is confirmed by the higher relative changes in tree species abundances in presence of all herbivores. Furthermore, since Sand Forest is a climax type (Matthews 2005), such competition among trees should not lead to changes in tree species composition.

Foraging activities by herbivores can open up the forest (Shannon *et al.* 2009) and provide an opportunity for tree species from other habitats to colonise Sand Forest (Matthews 2005). This habitat transformation can occur when savanna tree species colonise gaps within the forest,

causing irreversible change toward savanna woodland, thereby endangering the persistence of Sand Forest community in Southern Africa. This illustrates the importance which a shift in tree species may have for the sustainability of Sand Forest.

The study has demonstrated that browsing release by larger-size herbivores (*e.g.* either elephant or nyala) affects resource utilisation by their smaller counterparts (*e.g.* either nyala or small-size herbivores). For example, after the exclusion of their larger counterparts, resource specificity and browsing pressure by nyala and small-size herbivores increased. The diets among the different-size herbivores were segregated as there was little diet overlap among the different groups where all were present. This is consistent with Makhabu (2005), who found that elephant utilise different tree resources compared to 'smaller'-size herbivores (*e.g.* kudu and impala). However, one would expect overlap to decrease as specificity increases for any particular pair of guild members. Contrary to this, those species with the highest specificity (nyala and small-size browsers) also showed the highest overlap.

Interspecific competition theory (Gordon & Illius 1989) predicts diet overlap between different herbivore species to be lower when resources are scarce as herbivores must be more selective to optimise their nutritional intake, and compete for resources (Weisberg *et al.* 2006). In contrast, when resource availability is high, diet overlap is expected to increase. Diet overlap was indeed low where all herbivores were present, though the increased diet overlap between nyala and small-size herbivores in the partial enclosure (elephant absent) was not significantly different to the full access treatment (*cf.* Makhabu 2005). However, for smaller herbivores (*i.e.* nyala and small-size herbivores) we found a dietary shift (*i.e.* increase in resource specificity) and an increase in browsing pressure, after browsing release from their larger counterparts (elephant and nyala respectively). This could result from structural changes to the vegetation (*e.g.* increase in resource availability within the browsing height of the smaller-size herbivores (*cf.* Moe *et al.* 2009)), and suggests competitive displacement with larger-size herbivores (Stewart *et al.* 2002) where all herbivore species are present. Increased exclusive tree species use in the absence of their larger counterparts may contribute to a change in tree species assemblages, as observed for the partial enclosure for nyala. The lower browsing pressure by small-size herbivores (*i.e.* small-size herbivores and/or nyala), which occurs where larger herbivores (*i.e.* nyala and/or elephant) were present, could be a behavioural response towards these larger herbivore species, *i.e.* interference competition (Kerley *et al.* 2008).

While interference competition might take place, small-size herbivores can still efficiently compete with larger-size herbivores (Woolnough & Du Toit 2001, Cameron & Du Toit 2007). In turn, large herbivores facilitate mesoherbivores, increasing browse availability at lower levels, after impacting on large trees (Rutina *et al.* 2005, Makhabu *et al.* 2006a, Kohi *et al.* 2011: elephant facilitating impala). The fact that elephant, nyala and small-size herbivores utilise Sand Forest patches in Phinda shows these herbivores are able to coexist. We have not found evidence yet of elephant facilitating meso- or small-size herbivores, probably because elephant are unable to push over the tall trees, or break branches to ground level. However we believe that there is facilitation from mesoherbivores, such as nyala. Their browsing activity maintains vegetation in a suppressed “hedge” or coppice form (Smallie & O’Connor 2000, Lagendijk *et al.* 2011). Thus mesoherbivores facilitate both themselves (*cf.* de Knecht *et al.* 2008) and small-size herbivores by retaining sufficient browse availability, which otherwise would have grown past their feeding height.

Two years of herbivore exclusion is a short interval over which to observe well established changes in vegetation composition, and unfortunately it is nearly impossible to initiate an experiment in a natural system where tree species assemblages are concordant in all treatments at the start of the study. Regardless, we demonstrated short-term effects on tree species assemblages (*cf.* Jachmann & Croes 1991) after browsing/herbivore release. Future surveys of our experimental plots will elucidate the more complex mechanisms that appear to be at work here (*e.g.* interspecific competition among herbivores and among tree species, and interference competition), over a longer-term treatment duration.

The indirect effect of active herbivore management on both tree species assemblages and smaller-size herbivores in multi-species mammalian herbivore communities can have profound impact on ecosystems. Especially in habitats which are low in herbivore species diversity (such as Sand Forest (Matthews 2005)), the absence of one key species can have strong effects not diffused by other similar-size herbivore species present in more diverse systems (*cf.* Schmitz *et al.* 2000, Goheen *et al.* 2007). This can result in cascading effects where changes in one or more herbivore species alter the abundance of others (Ripple & Beschta 2007), with consequent changes at lower trophic levels (*e.g.* tree availability and composition). We demonstrated that browsing release by different-size herbivores changes tree species assemblages in Sand Forest. These changes could potentially cascade into the invertebrate level (one of our future research endeavours). Such cascading effects in Sand Forest were shown by alterations in dung beetle and spider assemblages

after vegetation structure changed due to elephant disturbance (Botes *et al.* 2006, Haddad *et al.* 2010).

Therefore, consequent changes in tree species assemblages can have several implications for the ecosystem. Firstly, it can alter vegetation dynamics (Cadenasso *et al.* 2002), as plant-plant interactions, and thus growth, change under different compositions. Secondly, it affects biodiversity, with the loss or gain of tree species and consequent change in animal species which may be dependent on specific trees (Kerley *et al.* 2008). Finally, changes in tree species assemblages can cascade into ecosystem processes, such as nutrient cycling (Hobbs 1992, Chapin *et al.* 2000). Subsequent changes in ecosystem processes again feed back into higher trophic levels. Hence, altered ecosystem processes can jeopardise the sustainability and survival of the ecosystem in its current ecological state.

At a time when human activities and conservation are competing for land, it is imperative to make well-informed management decisions. Conservation management strategies need to consider the role of the full herbivore assemblage present, and the effects of removal, introduction, or decrease of one or more herbivore species, in order to conserve habitats and biodiversity across all trophic levels.

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### **References**

- AUGUSTINE, D. J. and MCNAUGHTON, S. J. 2004. Regulation of shrub dynamics by native browsing ungulates on East African rangeland. *J. Appl. Ecol.* 41: 45-58.
- BAKKER, E. S., RITCHIE, M. E., OLFF, H., MILCHUNAS, D. G. and KNOPS, J. M. H. 2006. Herbivore impact on grassland plant diversity depends on habitat productivity and herbivore size. *Ecology Letters* 9: 780-88.

- BOND, W. J. and LOFFELL, D. 2001. Introduction of giraffe changes acacia distribution in a South African savanna. *Afr. J. Ecol.* 39: 286-94.
- BOND, W. J., SMYTHE, K. A. and BALFOUR, D. A. 2001. Acacia species turnover in space and time in an African savanna. *J. Biogeogr.* 28: 117-28.
- BOTHMA, J. D. P., VAN ROOYEN, N. and VAN ROOYEN, M. W. 2004. Using diet and plant resources to set wildlife stocking densities in African savannas. *Wildlife Society Bulletin* 32: 840-51.
- BOTES, A., MCGEOCH, M. A. and VAN RENSBURG, B. J. 2006. Elephant- and human-induced changes to dung beetle (Coleoptera: Scarabaeidae) assemblages in the Maputaland Centre of Endemism. *Biol. Conserv.* 130: 573-83.
- CADENASSO, M.L., PICKETT, S.T.A., and MORIN, P.J. 2002 Experimental test of the role of mammalian herbivores on old field succession; community structure and seedling survival. *Journal of the Torrey Botanical Society* 129: 228-237.
- CAMERON, E. Z. and DU TOIT, J. T. 2007. Winning by a neck: Tall giraffes avoid competing with shorter browsers. *Am. Nat.* 169: 130-135
- CARDOSO, P., BORGER, P. A. V. and VEECH, J. A. 2009. Testing the performance of beta diversity measures based on incidence data: the robustness to undersampling. *Diversity and Distributions* 15: 1081-90.
- CARRUTHERS, J., BOSHOFF, A., SLOTOW, R., BIGGS, H. C., AVERY, G., MATTHEWS, W. 2008. The elephant in South Africa: history and distribution. *In* R. J. SCHOLE, MENNELL, K.G. (eds). *Elephant Management: A Scientific Assessment for South Africa*, pp. 23-84. Witwatersrand University Press, Johannesburg, South Africa.
- CHAPIN, F. S., ZAVALA, E. S., EVINER, V. T., NAYLOR, R. L., VITOUSEK, P. M., REYNOLDS, H. L., HOOPER, D. U., LAVOREL, S., SALAI, O. E., HOBBI, S. E., MACK, M. C. and DÍAZ, S. 2000. Consequences of changing biodiversity. *Nature* 405: 234-42.
- CLARKE K. R. and WARWICK, R. M. 2001 Change in marine communities: an approach to statistical analysis and interpretation. Plymouth, UK: PRIMER-E.
- DE GARINE-WICHATITSKY, M., FRITZ, H., GORDON, I. J. and ILLIUS, A. W. 2004. Bush selection along foraging pathways by sympatric impala and greater kudu. *Oecologia* 141: 66-75.
- DE KNEGT, H. J., GROEN, T. A., VAN DE VIJVER, C. A. D. M., PRINS, H. H. T. and VAN LANGEVELDE, F. 2008 Herbivores as architects of savannas: inducing and modifying spatial vegetation patterning. *Oikos* 117: 543-554.

- DRUCE, H.C., PRETORIUS, K., DRUCE, D. and SLOTOW, R. 2006 The effect of mature elephant bull introductions on ranging patterns of resident bulls: Phinda Private Game Reserve, South Africa. *Koedoe* 49: 77-84.
- DRUCE, H.C., PRETORIUS, K. and SLOTOW, R. 2008 The response of an elephant population to conservation area expansion: Phinda Private Game Reserve, South Africa. *Biol Conserv* 141: 3127-3138.
- DU TOIT, J. T. 1995. Determinants of the composition and distribution of wildlife communities in Southern Africa. *Ambio* 241: 2-6.
- DU TOIT, J. T. and CUMMING, D. H. M. 1999. Functional significance of ungulate diversity in African savannas and the ecological implications of the spread of pastoralism. *Biodiv. Conserv.* 8: 1643-61.
- FRITZ, H., DUNCAN, P., GORDON, I. J. and ILLIUS, A. W. 2002. Megaherbivores influence trophic guilds structure in African ungulate communities. *Oecologia* 131: 620-25.
- GILL, R. M. A. and BEARDALL, V. 2001. The impacts of deer on woodlands: the effects of browsing and seed dispersal on vegetation structure and composition. *Forestry* 743: 209-18.
- GOHEEN J. R., KEESING, F., ALLAN, B. F., OGADA, D., and OSTFELD, R.S. 2004. Net effects of large mammals on *Acacia* seedling survival in an African savanna. *Ecology* 85: 1555-1561.
- GOHEEN, J. R., YOUNG T. P., KEESING, F. and PALMER, T. M. 2007. Consequences of herbivory by native ungulates for the reproduction of a savanna tree. *J. Ecol.* 95: 129-138.
- GORDON, I. J. and ILLIUS, A. W. 1989. Resource partitioning by ungulates on the Isle of Rhum. *Oecologia* 793: 383-89.
- GOTELLI, N. J. and ENTSMINGER, G. L. 2004. EcoSim: Null models software for ecology. Version 7.0. Acquired Intelligence Inc. and Kesity-Bear. Jericho, VT 05465. Available at [http://homepages.together.net/~gentsmin/eco\\_sim.htm](http://homepages.together.net/~gentsmin/eco_sim.htm) (accessed November 17, 2009)
- GULDEMOND, R. A. R. and VAN AARDE, R. J. 2007. The impact of elephants on plants and their community variables in South Africa's Maputaland. *Afr. J. Ecol.* 45: 327-35.
- GUSSET, M., RYAN, S. J., HOFMEYR, M., VAN DYK, G., DAVIES-MOSTERT, H. T., GRAF, J., OWEN, C., SZYKMAN, M., MACDONALD, D. W., MONFORT, S. L., WILDT, D. E., MADDOCK, A. H., MILLS, M. G. L., SLOTOW, R. and SOMERS, M. J. 2008. Efforts going to the dogs? Evaluating attempts to re-introduce endangered wild dogs in South Africa. *J. Appl. Ecol.* 45: 100-08.

- HADDAD, C., HONIBALL, A. S., DIPPENAAR-SCHOEMAN, A. S., SLOTOW, R. and VAN RENSBURG, B. J. 2010. Spiders as potential indicators of elephant-induced habitat changes in endemic sand forest, Maputaland, South Africa. *Afr. J. Ecol.* 48: 446-460.
- HOBBS, T. N. 1996. Modification of ecosystems by ungulates. *Journal of Wildlife Management* 60: 695-713.
- HOOPER, D. U. and VITOUSEK, P. M. 1997. The effects of plant composition and diversity on ecosystem processes. *Science* 277:1302-1305.
- JACHMANN, H. and CROES, T. 1991. Effects of browsing by elephants on the *Combretum/Terminalia* woodland at the Nazinga Game Ranch, Burkina Faso, West Africa. *Biol. Conserv.* 57: 13-24.
- JACKSON, D.A. 1995. PROTEST: A PROcrustean Randomization TEST of community environment concordance. *Ecoscience* 2:297-303.
- KAREIVA, P. 1982. Exclusion experiments and the competitive release of insects feeding on collards. *Ecology* 63: 696-704.
- KERLEY, G. I. H., LANDMAN, M., KRUGER, L., OWEN-SMITH, N., BALFOUR, D., DE BOER, W. F., GAYLARD, A., LINDSAY, K. and SLOTOW, R. 2008. Effects of elephants on ecosystems and biodiversity. *In* R. J. SCHOLE, MENNELL, K.G. (eds) *Elephant Management: A Scientific Assessment for South Africa*, pp. 146-205. Witwatersrand University Press, Johannesburg, South Africa.
- KING, J. R. and JACKSON, D. A. 1999. Variable selection in large environmental data sets using principal components analysis. *Environmetrics* 10:67-77.
- KIRBY, T., SHANNON, G., PAGE, B. and SLOTOW, R. 2008. The influence of sexual dimorphisms on the foraging behaviour of the nyala *Tragelaphus angasii*. *Acta Zool. Sin.* 54: 561-68.
- KIRKWOOD, D. and MIDGLEY, J. J. 1999. The floristics of Sand Forest in northern KwaZulu-Natal, South Africa. *Bothalia* 29: 293-304.
- KOHI, E. M., DE BOER, W. F., PEEL, M. J. S., SLOTOW, R., VAN DER WAAL, C., HEITKONIG, I. M. A., SKIDMORE, A., AND PRINS, H. H. T. 2011. African elephants *Loxodonta africana* amplify browse heterogeneity in African savanna. *Biotropica*. DOI: 10.1111/j.1744-7429.2010.00724.x)
- KOLEFF, P., GASTON, K. J. and LENNON, J. J. 2003. Measuring beta diversity for presence-absence data. *J. Anim. Ecol.* 72: 367-82.
- LAGENDIJK, D. D. G, MACKEY, R. M., PAGE, B. R. AND SLOTOW, R. (2011). The Effects of Herbivory by a Mega- and Mesoherbivore on Tree Recruitment in Sand Forest, South Africa. *PLoS ONE* 6(3): e17983. DOI:10.1371/journal.pone.0017983E.

- LEVICK, S. and ROGERS, K. 2008. Patch and species specific responses of savanna woody vegetation to browser exclusion. *Biol. Conserv.* 141: 489-98.
- LEVICK, S., ASNER, G. P., KENNEDY-BOWDOIN, T. and KNAPP, D. E. 2009. The relative influence of fire and herbivory on savanna three-dimensional vegetation structure. *Biol. Conserv.* 142: 1693-700.
- LEVINS, R. 1968. *Evolution in changing environments: Some theoretical explorations.* Princeton University Press, Princeton, U.S.A.
- MAKHABU, S. W. 2005. Resource partitioning within a browsing guild in a key habitat, the Chobe Riverfront, Botswana. *J. Trop. Ecol.* 21: 641-49.
- MAKHABU, S. W., SKARPE, C., HYTTEBORN, H. 2006a. Elephant impact on shoot distribution on trees and on rebrowsing by smaller browsers. *Acta Oecologica* 30: 136-146.
- MAKHABU S. W., SKARPE, C., HYTTEBORN, H. AND MPOFU, Z. D. 2006b. The plant vigour hypothesis revisited - how is browsing by ungulates and elephant related to woody species growth rate? *Plant Ecol.* 184: 163-172.
- MATTHEWS, W. S., VAN WIJK, A. E., VAN ROOYEN, N. and BOTHA, G. A. 2001. Vegetation of Tembe Elephant Park, Maputaland, South Africa. *S. Afr. J. Bot.* 67: 573-94.
- MATTHEWS, W. S. (2005) *Contributions to the ecology of Maputaland, southern Africa, with emphasis on Sand Forest.* PhD dissertation, University of Pretoria.
- MOE, S. R., RUTINA, L. P., HYTTEBORN, H. and DU TOIT, J. T. 2009. What controls woodland regeneration after elephants have killed the big trees? *J. Appl. Ecol.* 46: 223-230.
- MOLL, E.J. 1980. Terrestrial plant ecology. *In* M.N. BRUTON, COOPER K.H. (eds) *Studies on the ecology of Maputaland* pp. 52-68. Rhodes University & The Natal Branch of the Wildlife Society of Southern Africa, Grahamstown and Durban, South Africa.
- MORGAN, S., MACKEY, R. L. and SLOTOW, R. 2009. A priori valuation of land use for the conservation of black rhinoceros (*Diceros bicornis*). *Biol. Conserv.* 142: 384-393.
- MUCINA, L. and RUTHERFORD, M. C. (eds) 2006. *The Vegetation of South Africa, Lesotho and Swaziland.* Strelitzia 19. South African National Biodiversity Institute, Pretoria, South Africa.
- OLOFSSON, J., HULME, P. E., OKSANEN, L. and SUOMINEN, O. 2004. Importance of large and small mammalian herbivores for the plant community structure in the forest tundra ecotone. *Oikos* 106: 324-34.
- OWEN-SMITH, R. N. 1988. *Megaherbivores: the influence of very large body size on ecology.* Cambridge University Press, Cambridge, UK.

- PACE, M. L., COLE, J. J., CARPENTER, S. R. and KITCHELL, J. F. 1999 Trophic cascades revealed in diverse ecosystems. *TREE* 14: 483-88.
- PERES-NETO, P. R. and JACKSON, D. A. 2001. How well do multivariate data sets match? The advantages of a Procrustean superimposition approach over the Mantel test. *Oecologia* 129:169-178.
- PIANKA, E. R. 1973. The structure of lizard communities. *Annu. Rev. of Ecol. Syst.* 4: 53-74.
- PRINS H.H.T., DE BOER W.F., VAN OEVEREN H., CORREIA A.U., MAFUCA J.M. and OLF, H. (2006) Co-existence and niche segregation of three small bovid species in southern Mozambique. *Afr. J. Ecol.* 44:186-198.
- PRINS, H. H. T. and DOUGLAS-HAMILTON, I. 1990. Stability in a multi-species assemblage of large herbivores in East Africa. *Oecologia* 83: 392-400.
- RIPPLE, W. J. and BESCHTA, R. L. 2007. Restoring Yellowstone's aspen with wolves. *Biol. Conserv.* 138: 514-19.
- RUTINA, L. P, MOE, S. R., and SWENSON, J. E. 2005. Elephant *Loxodonta africana* driven woodland conversion to shrubland improves dry-season browse availability for impalas *Aepyceros melampus*. *Wildlife Biology* 11: 207-213.
- SCHMITZ, O. J., HAMBÄCK, P. A. and BECKERMAN, A. P. 2000. Trophic cascades in terrestrial systems: a review of the effects of carnivore removals on plants. *Am. Nat.* 155: 141-53.
- SIEBERT, S. J., FISH, L., UIRAS, M. M. and IZIDINE, S. A. 2004. Grass assemblages and diversity of conservation areas on the coastal plain south of Maputo Bay, Mozambique. *Bothalia* 34: 61-71.
- SHANNON G., MATTHEWS W. S., PAGE B. R., PARKER G. E. and SMITH, J. R. 2009. The affects of artificial water availability on large herbivore ranging patterns in savanna habitats: a new approach based on modelling elephant path distributions. *Diversity and Distributions* 15: 776-83.
- SHAW, M. T., KEESING, F. and OSTFELD, R. S. 2002. Herbivory on Acacia seedlings in an East African savanna. *Oikos* 98: 385-392.
- SLOTOW, R., GARAI, M. E., REILLY, B., PAGE, B. and CARR, R. D. 2005. Population dynamics of elephants re-introduced to small fenced reserves in South Africa. *S. Afr. J. Wildl. Res.* 35: 23-32.
- SMALLIE, J.J. and O'CONNOR, T. G. 2000. Elephant utilization of *Colophospermum mopane*: possible benefits of hedging. *Afr. J. Ecol.* 38:352-359.

- SMART, N. O. E., HATTON, J.C. and SPENCE, D. H. N. 1985. The effects of long-term exclusion of large herbivores on vegetation in Murchison Falls National Park, Uganda. *Biol. Conserv.* 33: 229-45.
- STEWART, K. M., BOWYER, R. T., KIE, J. G., CION, N. J. and JOHNSON, B. K. 2002. Temporospatial distributions of elk, mule deer, and cattle: resource partitioning and competitive displacement. *J. Mammal.* 83: 229-44.
- TILMAN, D., KNOPS, J. M. H., WEDIN, D., REICH, P., RITCHIE, M. and SIEMANN, E. 1997. The influence of functional diversity and composition on ecosystem processes. *Science* 277: 1300-1302.
- TRINKEL, M., FERGUSON, N., REID, A., REID, C., SOMERS, M. J., TURELLI, L., GRAF, J., SZYKMAN, M., COOPER, D., HAVERMAN, P., KASTBERGER, G., PACKER, C. and SLOTOW, R. 2008. Translocating lions into an inbred lion population in the Hluhluwe-iMfolozi Park, South Africa. *Animal Conservation* 11: 138-43.
- WALKER, B. H. 1976. An approach to the monitoring of changes in the composition and utilization of woodland and savanna vegetation. *S. Afr. J. Wildl. Res.* 6: 1-32.
- WEISBERG, P. J., COUGHENOUR, M. B. and BUGMANN, H. 2006. Modelling of large herbivore-vegetation interactions in a landscape context. *In* K. Danell, Bergström, R., Duncan, P. and Pastor, J. (eds) *Large herbivore ecology ecosystem dynamics and conservation*, pp. 348-382. Cambridge University Press, Cambridge, UK.
- WISEMAN, R., PAGE, B. R. and O'CONNOR, T. G. 2004. Woody vegetation change in response to browsing in Ithala Game Reserve, South Africa. *S. Afr. J. Wildl. Res.* 34: 25-37.
- WOOLNOUGH, A. P. and DU TOIT, J. T. 2001. Vertical zonation of browse quality in tree canopies exposed to a size-structured guild of African browsing ungulates. *Oecologia* 129: 585-590.
- YOUNG, T. P., OKELLO, B., KINYUA, D. and PALMER, T. 1998. KLEE: a long-term multi-species herbivore exclusion experiment in Laikipia, Kenya. *African Journal of Range and Forage Science* 14: 92-104.

## CHAPTER 6

### General Discussion

Although herbivores are recognised to be a major determinant in shaping our terrestrial environments (Scholes & Walker 1993; Seymour 2008), the relative effects of herbivory (i.e. browsing herbivores) on vegetation, and the potential browsing interaction with other species still remain unclear. The general aim of this dissertation was therefore to gain a better understanding of the browsing effects from mega- and mesoherbivores on vegetation and other herbivore species; such understanding could contribute to decision making processes within conservation management. I mainly did this through the use of enclosure experiments. Conducting these experiments in Africa provided the opportunity to separate browsing effects among herbivores of different sizes: a megaherbivore, the African elephant *Loxodonta africana*, and mesoherbivores, such as impala *Aepyceros melampus* and nyala *Tragelaphus angasii*. The inclusion of elephant into the study presented the opportunity to assess, more in-depth, the impact elephant can exert on the vegetation, which is of current concern to elephant management in Southern Africa due to population increases (Kerley et al. 2008; Kalwij et al. 2010). I specifically focused on the effect of elephant on tree densities within various height classes. In addition, I could also examine how elephant, through its presence or absence, can affect browsing patterns of other herbivores. Studies testing the effect of megaherbivore release have been few, and also, the effect of mesoherbivores on vegetation is not yet fully understood.

Chapter 2 demonstrates that woody plant densities among protected savanna areas were variable, and different tree size classes were not always represented by all species, and were thus missing from the landscape. Both regional (i.e. rainfall) and local drivers (i.e. fire and elephant) were important determinants of woody densities in savannas (Chapter 2). Interestingly, the time since elephant were present affected woody densities within size classes more than actual elephant densities. The loss of medium or large reproductive trees due to elephant driven mortality, can eventually be reflected in relatively lower recruitment rates, which effects take time to move through different life-stages. Sand Forest regeneration was impacted by nyala only and both elephant and nyala in combination, but not by elephant only (Chapter 4). Short term elephant and/or nyala exclusion caused a change in woody species composition in Sand Forest (Chapter 5), while woody species composition remained similar with recent elephant access in savanna (Chapter 3). Elephant displaced mesoherbivores, both in savanna and Sand Forest, thereby negatively affecting mesoherbivore browsing patterns (Chapter 3 and 5). Browsing events for

mesoherbivores were lower with elephant, than in elephant absence, which in savanna resulted higher sapling densities (Chapter 3). Most importantly, in contrast to most other exclosure experiments (e.g. Goheen et al. 2007; Levick & Rogers 2008; Siebert & Eckhardt 2008; Riginos & Young 2007), the Sand Forest experiment (Chapter 4 and 5) elucidated single species effects (i.e. nyala or elephant). The recognition of both single and multispecies effects is imperative when managing multispecies assemblages to avoid inappropriate management.

### **Vegetation dynamics**

At the global scale there is concern about the increase in woody thickening or bush encroachment due to climate change (Wigley et al. 2010). By contrast, at the regional scale in South Africa the decrease or loss of especially large trees, by elephant, is of concern (Ben-Shahar 1998; Eckhardt et al. 2000; Kalwij et al. 2010), while at the local scale the problem is thought to be a lack of recruitment (e.g. Sand Forest (Matthews 2005)). Vegetation dynamics are inherently complex processes and influenced by many factors.

The previous notion that natural recruitment is a demographic bottleneck in Sand Forest (Matthews 2005) is misplaced as recruitment into the seedling phase takes place. However, the subsequent natural transition into the sapling phase is inhibited by browsing pressure. This so-called browsing trap was observed in Sand Forest, and also in savanna (i.e. Ukhozi) where more saplings were present where impala were being displaced by elephant. Smaller sized herbivores, rodents and invertebrates also predate on seedlings, as indicated by studies from East African savannas (Shaw et al. 2002; Augustine & McNaughton 2004; Goheen et al. 2007). This has not yet been investigated in Sand Forest.

The transition of woody individuals through different stages of the population is inhibited by both mesoherbivores (Sand Forest) and megaherbivores (Sand Forest and savanna). It is important to acknowledge that tree populations are impacted in the early life stages by mesoherbivores as well as in the mature stages by elephant. While elephant have the ability to kill mature trees (Owen-Smith 1988; Kerley et al. 2008), and thus may affect recruitment (seedlings; Chapter 2) by reducing seed production by parent trees, mesoherbivores obstruct population dynamics by removing then viable recruits from the regeneration process. Thus, the specific effects of mesoherbivores should not be disregarded in assessing drivers of vegetation dynamics.

In addition, population structures are also affected by fire and rainfall (Chapter 2; cf. Higgins et al. 2000; Bond & Archibald 2003; Bond & Keeley 2005). Interactions exist between the different drivers. For example, fire and herbivory together have been found to decrease tree densities more than each driver alone (Staver et al. 2009). In savannas, the disruptions in tree size distributions appear to be mortality related (Chapter 2). Recruitment seems to be taking place, but the transition into taller size classes is impacted by fire and elephant. Regeneration through all size classes is imperative, to guarantee a pool of reproductive trees within the population, to compensate for natural die-offs, impact of fire and herbivores. A disrupted transition process retards the increase in reproductive trees, and thus negatively affects recruitment rates. A hiatus within the demographic process of a tree population can potentially ultimately lead to the local extirpation of species, or even the conversion of savanna woodland to grasslands (cf. Van de Koppel & Prins 1998). This in its turn will cause a shift in herbivore assemblages (e.g. browser/mixed feeder towards grazers; Van de Koppel & Prins 1998; Fritz et al. 2002; Codron et al. 2007).

Elephant affected tree species composition in Sand Forest, but not in savanna. Especially the latter is in contrast to the literature, where changes in vegetation composition have been reported both in short-term and long-term exclusion of elephant (Owen-Smith 1988; Augustine & McNaughton 2004; Levick & Rogers 2008). This may be an elephant density effect, or perhaps the existing savanna vegetation was resilient against short-term elephant impact. Woody species composition in Sand Forest was also affected by nyala, suggesting nyala may be an agent of habitat change. The experimental design in savanna was not set up to detect an impala-effect. Studies from Botswana and Tanzania have indicated an effect of impala on recruitment of species (Prins & Van der Jeugd 1993; Skarpe et al. 2004, Moe et al. 2009), but their impact on woody species composition remains unknown. The unfavourable effects which both fire and herbivory exhibit, on both population dynamics and species composition, indicate the need for a temporal fire- and browsing release in order for woody individuals to escape the browse trap and be able to grow into taller height classes (Staver et al. 2009). Herbivore dynamics can be negatively affected by drought or disease (Prins & Van der Jeugd 1993; Skarpe et al. 1994). However, the temporal occurrence of these natural events may be too sparse to achieve a viable window for woody plant recruitment and transition into taller cohorts, as herbivore densities are high in fenced-off protected areas (see 'Conservation Management' below). This would therefore necessitate a management driven herbivory (or fire) release.

### **Facilitation and displacement**

Contrasting results have been reported in the literature concerning the effect of elephant on other herbivores. Elephant may facilitate mesoherbivores, increasing forage availability at lower height levels through feeding on larger trees (Rutina et al. 2005; Makhabu et al. 2006; Kohi et al. 2011). In a recent study conducted by Valeix et al. (2011) in Hwange National Park, Zimbabwe, impala were found to prefer habitats which were previously impacted by elephant leading to structural changes to the vegetation (e.g. coppiced, broken and uprooted trees). Elephant-induced vegetation changes increased the availability of forage and visibility (i.e. a seemingly lower perceived predation risk; Valeix et al. 2011). I did not find evidence for this type of facilitation in Sand Forest or savanna. The areas available to elephant in Sand Forest are relatively open, but were not more intensively utilised by nyala (based on my browsing pressure data). Also, forage availability in these areas was not increased as trees are too tall to break or push over (i.e. max tree height recorded 25 m). Perhaps the time scale in my savanna experiment (i.e. Ukhozi) was too short to significantly increase forage availability and visibility, but then there was also a significant difference in elephant densities between Ukhozi and Hwange National Park ( $1.17 \text{ km}^{-2}$  and  $2\text{-}5 \text{ km}^{-2}$  respectively; Chapter 3 and Valeix et al. 2011). Facilitation may therefore perhaps be a function of time since exposure to elephant and elephant densities, i.e. similarly to my result for the effect on population structure (Chapter 2). This indicates that scientific and management attention should not only include elephant densities, but also the time since elephants have been present.

In contrast to facilitation, a meta-analysis by Fritz et al. (2002), and a separate study by Valeix et al. (2007a), showed that where megaherbivores are more abundant mesoherbivores decline, presumably through habitat change or competition for forage resources (Fritz et al. 2002; Valeix et al. 2011). My results from Sand Forest and savanna indicate behavioural displacement as a third potential mechanism for the observed patterns. Displacement by elephant has been previously observed at waterholes (Valeix et al. 2007b). Perhaps in savannas, when elephant have gained recent access to an area, displacement of other herbivore species occurs. Then, once elephant utilisation continues for a longer period of time, elephant-induced changes to the vegetation structure, increases forage availability and visibility for other herbivores, thereby providing a facilitating effect. However, because of the spatial scaling, I expect displacement pressure to be lower in savannas, than in Sand Forest. Sand Forest occurs in a mosaic of small patches (e.g.  $5.2 \text{ km}^2$ ; Chapter 5; Matthews 2005; Kellerman & Van Rooyen 2007), and may as such have a similar displacement effect as waterholes (Valeix et al. 2007b) due to their relatively small size compared to savanna areas. This requires further scientific attention.

Mesoherbivores did facilitate smaller sized herbivores, and themselves (i.e. self-facilitation) in Sand Forest, by maintaining the vegetation within accessible and preferred browsing height. This chronic (re)browsing again leads to the persistent browsing trap (sensu Bond & Archibald 2003) impeding natural regeneration of trees. To my knowledge, facilitation of smaller sized herbivores by mesoherbivores has not yet been described.

### **The cascading effects of herbivore release**

The mechanisms of trophic cascades due to browsing release were experimentally confirmed in Sand Forest. The balance between co-existing herbivores may be disturbed through active management (e.g. population reductions, removal or introduction). This can result in cascading effects where changes in one or more species alter the abundance of others (Ripple & Beschta 2007), with consequent changes at lower trophic levels (e.g. plant resource availability and composition). Potentially, this may even affect ecosystem processes (Hooper & Vitousek 1997; Tilman et al. 1997).

In Sand Forest, the indirect human-induced cascading effect onto lower trophic levels was demonstrated as tree species assemblages had changed and recruitment was inhibited after the removal of nyala, and/or elephant (Chapter 4 and 5). The further consequences of this were observed in and around Tembe Elephant Park, South Africa, where assemblages of both dung beetles (Botes et al. 2006) and spiders (Haddad et al. 2010) were altered after elephant-induced vegetation changes. Besides their well documented effects on vegetation (e.g. Kerley et al. 2008, Kirby et al. 2008), this illustrates the broader effects of herbivory by elephant (and nyala), i.e. on smaller sized herbivores, and cascading into invertebrate levels. Thus, the indirect cascading effects of active management, especially on species composition, become critical as they affect vegetation dynamics, biodiversity and ecosystem processes, endangering the sustainability of the ecosystem.

### **Conservation management**

This thesis showed that both elephant and mesoherbivores exert direct and indirect (i.e. displacement, providing a window for recruitment) impact on vegetation, in addition to rainfall (Higgins et al. 2000; Kraaij & Ward 2006; Sankaran et al. 2008) and fire (Bond et al. 2001; Bond & Archibald 2003; Levick et al. 2009). The diversity of drivers affecting ecosystems, and the differential ecological responses across systems, makes protection and management of areas an extremely complex task. In protected areas, disturbances (i.e. fire and herbivory) have

significantly altered from historical natural regimes (Bond & Keeley 2005). Burning is actively applied (Van Wilgen et al. 2004; Bond & Keeley 2005) instead of natural lightning-induced fires (Bond & Keeley 2005), and the introduction of more game and subsequent increase in numbers (e.g. Bond & Loffell 2001; Mackey et al. 2006) has intensified the herbivory pressure within protected areas. Although disturbances are intrinsic to ecosystems, the amplified extent of disturbances, due to management and fencing-off areas, may far exceed the ecological resilience thresholds of certain ecosystems to cope with these disturbances (cf. Owen-Smith 1988).

The implications which arise from this thesis, in particular in view of the current elephant debate in Southern Africa (Scholes & Mennell 2008), are that both elephant and mesoherbivores require sound management to promote sustainable tree population demographics. Management plans thus need to include all herbivore species when setting targets for conservation. Adaptive active management (i.e. removal, introduction or reductions of densities and herbivore species) will be more crucial in smaller protected areas ( $< 900 \text{ km}^2$ ; Slotow et al. 2005) as herbivore populations increase, and effects become more pronounced when spatial dispersion is limited (Owen-Smith et al. 2006; Kerley et al. 2008).

Active fire (e.g. longer fire return periods) and herbivore management (e.g. browsing release through exclusion) will benefit population structures of many plant species. This may be more important in the early recruitment stage when both fire and herbivory prevent transition into the next height class (Chapter 2, 3 and 4; cf. Belsky et al. 1984, Prins & Van der Jeugd 1993; Barnes 2001; Bond & Archibald 2003; Levick et al. 2009). Chapter 2 showed that densities of trees  $\leq 3$  m benefit from a prolonged fire return period. However, elephant impact on mature trees is also fundamental to consider to prevent the loss of reproductive trees. Protected areas, such as Kruger National Park, are conducting fire experiments to determine the effects of different fire regimes (Biggs et al. 2003). In addition, the spatial heterogeneity of burnt areas can be determined by management, and sensitive areas can, for example, be protected using fire breaks (sensu Van Wilgen et al. 2004). In Addo Elephant National Park, several botanical reserves have been established in sections of the park, to protect succulent thicket vegetation from browsing pressure (Lombard et al. 2001). Such a measure may be implemented in other areas, not only to prevent herbivory on tall trees by elephant but also to curb recruitment predation by mesoherbivores. Another measure against elephant damage which has proven successful, especially against debarking, is fencing the stems of tall trees with diamond mesh (Grant et al. 2008).

Contrasting results between protected areas, even within the same habitat, as well as of different drivers of savanna dynamics on specific height classes, call for the need to record any management measure taken, and to assess its effect on other species and vegetation. Collated data from many reserves and different management regimes can be used for meta-analysis purposes to improve our understanding of the effects of elephant and other herbivores on vegetation at different spatiotemporal scales and under various elephant densities. In addition, the information derived from more active monitoring of certain plant species at various spatial scales (e.g. reserve or regional scale) will allow conservation and management to respond to the effects of global change at all spatial scales.

Active and adaptive management of the herbivore species assemblage (i.e. the manipulation of densities) affect both vegetation and other herbivores and thus requires careful consideration of all consequences before implementation. Effects potentially cascade into lower trophic levels, jeopardising biodiversity and ecosystem processes. Therefore, the full herbivore assemblage present, and their combined and individual browsing effects need to be considered when setting management goals to conserve habitats and biodiversity across all trophic levels.

### **Limitations**

The studies described in this thesis have been carried out in two biomes (i.e. forest and savanna). I focussed on two different mesoherbivore species (i.e. nyala and impala) and experiments were used to exclude species (in Sand Forest; Chapter 4 and 5), but also allowed recent access (to elephant in savanna; Chapter 3). The dissimilarities between the study areas and species are such that I need to be cautious with the interpretation of the results and making inferences between studies. Habitats are known to respond differently to disturbance (Kerley et al. 2008). Also while both nyala and impala are mesoherbivores, nyala are larger in body size and have a different social structure than impalas (e.g. non territorial vs. seasonal territorial respectively; Estes 1991). This is expected to affect their foraging behaviour and thus impact on vegetation. Both the absence and presence of elephant has previously been observed to induce changes in vegetation (Kerley et al. 2008). However the question arises whether removal and introduction induce similar ecological responses. In this thesis I have found similar effects of herbivory and utilisation by different sized herbivores (e.g. increased browsing pressure in absence of larger counterparts both in Sand Forest as well as in savanna), as well as contrasting results between Sand Forest and savanna (e.g. species compositional change and increase in woody densities after elephant

browsing release vs. no change after short-term access). In addition, woody species also respond differently to disturbances such as fire and elephant (see chapter 2). Thus, caution is needed when extrapolating results between ecosystems and species, as similar disturbances may evoke differential ecological responses.

Interaction effects between drivers of vegetation dynamics in savannas (Eckhardt et al. 2000; Van Wilgen et al. 2004; Staver et al. 2009; Vanak et al. 2011) have not been included in this study as I was interested in single driver effects on different height classes within populations.

Data used in the savanna studies were collected during a single survey. Long-term monitoring is expensive in costs and time. Rates of change and processes driving population dynamics are therefore often inferred from static data (Obiri et al. 2002). Long-term monitoring programs are recommended to elucidate mechanisms and processes at work and confirm or reject results inferred from single surveys.

For Sand Forest I only reported results obtained from 2 years of herbivore release. This is too short to detect changes in overall tree populations, but was sufficient to indicate effects on recruitment, species composition and utilisation by other herbivores after browsing release. This experiment is being maintained for long-term monitoring and offers the opportunity to determine long-term browsing release effects in Sand Forest.

### **Gaps and future work**

The effect of mesoherbivores on vegetation dynamics has been largely overlooked, especially in conjunction with elephant presence in protected areas. Mesoherbivores affect regeneration of trees into taller size classes from bottom-up by preying on seedlings, while elephants impact on taller trees from top-down by pushing over and ring barking trees (Owen-Smith 1988; Kerley et al. 2008). When conserving areas of key importance, the effects of all (herbivore) species need to be considered before any active management. There are key areas which still require scientific attention as uncertainties of processes and mechanisms still prevail within and across ecosystems.

There is insight in the long-term impact elephants have on vegetation (e.g. habitat conversion; Rutina et al. 2005), but the short term effects of elephants, when areas are opened up, need further investigation in addition to the work presented in Chapter 3. Monitoring herbivory effects from the moment of introduction also allows for the determination of the rate at which vegetation

processes change, which still require a deeper understanding. The use of long-term monitoring is recommended. In addition to the rates of change, the lag effects of, for example, differences in rainfall regimes, elephant and mesoherbivore densities or the closing of waterholes on vegetation call for attention. In particular, the effects on recruitment and densities of reproductive trees are of interest.

A few studies used experimental designs to exclude elephant (and simultaneously other herbivores; Levick & Rogers 2008; Siebert & Eckhardt 2008 Riginos & Young 2007). However it is not clear, whether processes, and ecological responses, are similar when disturbances (e.g. elephant) are either introduced or removed.

The effect of other herbivores than nyala on recruitment needs quantification. Browsing release by impala was observed to facilitate shrub dynamics in Tanzania (Prins & Van der Jeugd 1993), but the majority of the work has been done on Botswana riverfront (Moe et al. 2009; Skarpe et al. 2004). Experimental research is needed in non-riverine savanna areas, to assess the impact of impala on regeneration of woody species in savannas. While recruitment within savannas appears to take place (Chapter 2), there may not be sufficient recruitment to replace the loss of taller trees impacted by increased elephant densities and applied fire regimes (Kerley et al. 2008; Bond & Keeley 2005). The concern of the decrease in densities and loss of taller, reproductive trees (Ben-Shahar 1998; Eckhardt et al. 2000; Kalwij et al. 2010) corroborates the suggestion that there nevertheless may be a recruitment problem. The extent or magnitude of browsing release by impala on savanna vegetation (i.e. recruitment and species composition) requires sound ecological research for a more complete understanding of the browsing effect of mesoherbivores on vegetation dynamics.

The contrasting results between facilitation and displacement raise the question at which densities and temporal scales displacement occurs. In addition, displacement of any herbivore species may have cascading effects on vegetation. Also, does displacement change into facilitation once elephant-induced changes have increased forage availability for mesoherbivores, and thus create a shift in the spatial utilisation by mesoherbivores? And after how long, and at what densities, does this switch take place?

Browsing effects are most often reported from studies focusing on single or similar-sized species (e.g. Belsky 1984, Jachman & Croes 1991). While these research endeavours are important,

ecosystems and herbivore communities consist of a number of (different-sized) species which, on their turn, can affect other biota and processes. The magnitude and complexity of changing communities, when multiple species are affected, are stronger since this affects multiple (a)biotic components and processes (e.g. species dependency for food sources, competition among plant species or altered nutrient cycling). However, opportunities to examine indirect multispecies effects are not only limited, but also challenging. The Sand Forest enclosure experiment will provide the opportunity to examine cascading effects of browsing release more closely.

Although this work was mainly focussed on the effects of herbivory on vegetation, the work in Sand Forest provided new insights into the ecology of this vulnerable ecosystem. As for now only short term effects were detected, the long-term set up of the experiment will allow for the monitoring of long-term herbivore exclusion effects on vegetation dynamics, and provide the opportunity for more in-depth research into Sand Forest ecology. Examples of future research endeavours would be to determine the predation effect of invertebrates and rodents on seedlings, the cascading effect of browsing release of different-sized herbivores on invertebrates, trophic cascades involving predators, herbivores and trees, and/or the potential facilitating effects of elephant paths (Shannon et al. 2009) and nyala trails for invasion from savanna species into the forest. While this later has been postulated (Shannon et al. 2009), empirical evidence is lacking. Sand Forest harbours many endemic plant and animal species (Matthews et al. 2001), making it a high priority that Sand Forest is preserved (Kirkwood & Midgley 1999; Matthews et al. 2001; Botes et al. 2006).

The above identified areas of research require research endeavours in many protected areas (i.e. site specific research; cf. Young et al. 2011) so as to be able to elucidate effects at different elephant/herbivore densities and in a wide range of habitats. Meta-analyses techniques can be used to detect browsing effect patterns at broader scales. Ecosystems are complex, and it is often inappropriate to extrapolate results of different studies between different localities. This is illustrated by the contrasting results, for example, between studies focussing on the effect of slope position on browsing patterns and vegetation (Chapter 3), as well as by the contrasting responses of woody densities to different drivers of savanna dynamics at various scales (Chapter 2). Collating data from different localities may also help us to understand whether increasing populations of elephant and mesoherbivores are causing irreversible changes to biodiversity, or simply accelerating the natural dynamic processes. Meta-analyses may facilitate the detection of species specific patterns, which may aid management at both the local and regional scale.

In addition, the reporting of non-detrimental results on any of these topics would be beneficial to create a complete understanding of the complexity of vegetation dynamics. Especially for elephant, published studies typically report negative effects (see Kerley et al. 2008). This creates a unidirectional bias in our understanding of herbivory effects at all spatial and temporal scales.

The human induced disturbances (e.g. manipulating population densities and fire regimes) and changes to the landscape have changed the natural ecological integrity. More importantly, decisions will have to be made whether to preserve the previous ecological state or to accept changes to the landscape and manage species populations to a level which is acceptable and sustainable for conservation of species at all trophic levels.

The proposed key research areas will contribute to the question what we need to conserve, protect and what is the best way to achieve this. In a world where the human footprint is everywhere we might have to accept certain losses of biodiversity. This does not necessary have to refer to global biodiversity. For instance, if a certain tree species is locally endangered in a protected area, but is regionally widespread (e.g. neighbouring reserve or country) the question needs to be raised if spending resources and management actions are really necessary to conserve this (and potential associated) species at this particular location (cf. O'Connor et al. 2007). We need to decide where our priorities lie. This thesis demonstrates that, for vegetation communities and structures, all possible drivers affecting vegetation need to be considered and not only the "obvious" and the "political" ones. Mesoherbivores play a much larger role in ecosystems than thus far acknowledged.

## References

- Augustine, D.J. & McNaughton, S.J. (2004) Regulation of shrub dynamics by native browsing ungulates on East African rangeland. *Journal of Applied Ecology*, 41, 45-58.
- Barnes, M.E. (2001) Effects of large herbivores and fire on the regeneration of *Acacia erioloba* woodlands in Chobe National Park, Botswana. *African Journal of Ecology*, 39, 340-350.
- Belsky, A.J. (1984) Role of small browsing mammals in preventing woodland regeneration in the Serengeti National Park, Tanzania. *African Journal of Ecology*, 22, 271-279.
- Ben-Shahar, R. (1998) Changes in structure of savanna woodlands in northern Botswana following the impacts of elephants and fire. *Plant Ecology*, 136, 189-194.

- Biggs, R., Biggs, H.C., Dunne, T.T., Govender, N. & Potgieter, A.L.F. (2003) Experimental burn plot trial in the Kruger National Park: history, experimental design and suggestions for data analysis. *Koedoe*, 46, 1-15.
- Bond, W.J. & Loffell, D. (2001) Introduction of giraffe changes acacia distribution in a South African savanna. *African Journal of Ecology*, 39, 286-294.
- Bond, W.J. & Archibald, S. (2003) Confronting complexity: fire policy choices in South African savanna parks. *International Journal of Wildland Fire*, 12, 381-389.
- Bond, W.J. & Keeley, J.E. (2005) Fire as a global 'herbivore': the ecology and evolution of flammable ecosystems. *Trends in Ecology and Evolution*, 20, 387-394.
- Bond, W.J., Smythe, K.A. & Balfour, D.A. (2001) Acacia species turnover in space and time in an African savanna. *Journal of Biogeography*, 28, 117-128.
- Botes, A., McGeoch, M.A. & Van Rensburg, B.J. (2006) Elephant- and human-induced changes to dung beetle (Coleoptera: Scarabaeidae) assemblages in the Maputaland Centre of Endemism. *Biological Conservation*, 130, 573-583.
- Eckhardt, H.C., van Wilgen, B.W. & Biggs, H.C. (2000) Trends in woody vegetation cover in the Kruger National Park, South Africa, between 1940 and 1998. *African Journal of Ecology*, 38, 108-115.
- Estes, R.D. (1991) *The behavior guide to African mammals: including hoofed mammals, canivores, primates*. University of California Press, Berkeley.
- Fritz, H., Duncan, P., Gordon, I.J. & Illius, A.W. (2002) Megaherbivores influence trophic guilds structure in African ungulate communities. *Oecologia*, 131, 620-625.
- Goheen, J.R., Young, T.P., Keesing, F. & Palmer, T.M. (2007) Consequences of herbivory by native ungulates for the reproduction of a savanna tree. *Journal of Ecology*, 95, 129-138.
- Grant, C.C., Bengis, R., Balfour, D., Peel, M., Davies-Mostert, H.T., Killian, H., Little, R., Smit, I., Garai, M.E., Henley, M., Anthony, B. & Hartley, P. (2008) Controlling the distribution of elephants. *Elephant Management: A Scientific Assessment for South Africa* (ed. by R.J. Scholes and K.G. Mennell), pp. 329-369. Witwatersrand University Press, Johannesburg.
- Haddad, C.R., Honiball, A.S., Dippenaar-Schoeman, A.S., Slotow, R. & Van Rensburg, B.J. (2010) Spiders as potential indicators of elephant-induced habitat changes in endemic sand forest, Maputaland, South Africa. *African Journal of Ecology*, 48, 446-460.
- Higgins, S.I., Bond, W.J. & Trollope, W.S.W. (2000) Fire, resprouting and variability: a recipe for grass-tree coexistence in savanna. *Journal of Ecology*, 88, 213-229.
- Hooper, D.U. & Vitousek, P.M. (1997) The effects of plant composition and diversity on ecosystem processes. *Science*, 277

- Jachmann, H. & Croes, T. (1991) Effects of browsing by elephants on the *Combretum/Terminalia* woodland at the Nazinga Game Ranch, Burkina Faso, West Africa. *Biological Conservation*, 57, 13-24.
- Kalwij, J.M., de Boer, W.F., Mucina, L., Prins, H.H.T., Skarpe, C. & Winterbach, C. (2010) Tree cover and biomass increase in a southern African savanna despite growing elephant population. *Ecological Applications*, 20, 222-233.
- Kellerman, M.J.S. & Van Rooyen, M.W. (2007) Seasonal variation in soil seed bank size and species composition of selected habitat types in Maputaland, South Africa. *Bothalia*, 37, 249-258.
- Kerley, G.I.H., Landman, M., Kruger, L., Owen-Smith, N., Balfour, D., de Boer, W.F., Gaylard, A., Lindsay, K. & Slotow, R. (2008) Effects of elephants on ecosystems and biodiversity. *Elephant Management: A Scientific Assessment for South Africa* (ed. by R.J. Scholes, Mennell, K.G.), pp. 146-205. Witwatersrand University Press, Johannesburg.
- Kirby, T., Shannon, G., Page, B. & Slotow, R. (2008) The influence of sexual dimorphisms on the foraging behaviour of the nyala *Tragelaphus angasii*. *Acta Zoologica Sinica*, 54, 561-568.
- Kirkwood, D. & Midgley, J.J. (1999) The floristics of Sand Forest in northern KwaZulu-Natal, South Africa. *Bothalia*, 29, 293-304.
- Kohi, E.M., de Boer, W.F., Peel, M.J.S., Slotow, R., Van der Waal, C., Heitkönig, I.M.A., Skidmore, A.K. & Prins, H. (2011) African elephants *Loxodonta africana* amplify browse heterogeneity in African savannas. *Biotropica*, DOI: 10.1111/j.1744-7429.2010.00724.x
- Kraaij, T. & Ward, D. (2006) Effects of rain, nitrogen, fire and grazing on tree recruitment and early survival in bush-encroached savanna, South Africa. *Plant Ecology*, 186, 235-246.
- Levick, S. & Rogers, K. (2008) Patch and species specific responses of savanna woody vegetation to browser exclusion. *Biological Conservation*, 141, 489-498.
- Levick, S., Asner, G.P., Kennedy-Bowdoin, T. & Knapp, D.E. (2009) The relative influence of fire and herbivory on savanna three-dimensional vegetation structure. *Biological Conservation*, 142, 1693-1700.
- Lombard, A.T., Johnson, C.F., Cowling, R.M. & Pressey, R.L. (2001) Protecting plants from elephants: botanical reserve scenarios within the Addo Elephant National Park, South Africa. *Biological Conservation*, 102, 191-203.

- Mackey, R.L., Page, B.R., Duffy, K.J. & Slotow, R. (2006) Modelling elephant population growth in small, fenced, South African reserves. *South African Journal of Wildlife Research*, 36, 33-43.
- Makhabu, S.W., Skarpe, C. & Hytteborn, H. (2006). Elephant impact on shoot distribution on trees and on rebrowsing by smaller browsers. *Acta Oecologica* 30:136-146.
- Matthews, W.S. (2005) *Contributions to the ecology of Maputaland, southern Africa, with emphasis on Sand Forest*. PhD, University of Pretoria, Pretoria.
- Matthews, W.S., Van Wijk, A.E., Van Rooyen, N. & Botha, G.A. (2001) Vegetation of Tembe Elephant Park, Maputaland, South Africa. *South African Journal of Botany*, 67, 573-594.
- Midgley, J.J., Everard, D.A. & Van Wyk, G. (1995) Relative lack of regeneration of shade-intolerant canopy species in some South African forests. *South African Journal of Science*, 91, 7-8.
- Moe, S.R., Rutina, L.P., Hytteborn, H. & Du Toit, J.T. (2009) What controls woodland regeneration after elephants have killed the big trees? *Journal of applied ecology*, 46, 223-230.
- O'Connor, T.G., Goodman, P.S. & Clegg, B. (2007) A functional hypothesis of the threat of local extirpation of woody plant species by elephant in Africa. *Biological Conservation*, 136, 329-345.
- Obiri, J.A.F., Lawes, M.J. & Mukolwe, M. (2002) The dynamics and sustainable use of high-value tree species of the coastal Pondoland forests of the Eastern Cape Province, South Africa. *Forest Ecology and Management*, 166, 131-148.
- Owen-Smith, N., Kerley, G.I.H., Page, B., Slotow, R. & Van Aarde, R.J. (2006) A scientific perspective on the management of elephants in the Kruger National Park and elsewhere. *South African Journal of Science*, 102, 389-394.
- Owen-Smith, R.N. (1988) *Megaherbivores: the influence of very large body size on ecology*. Cambridge University Press, Cambridge.
- Prins, H.H.T. & van der Jeugd, H.P. (1993) Herbivore Population Crashes and Woodland Structure in East Africa. *Journal of Ecology*, 81, 305-314.
- Riginos, C. & Young, T.P. (2007) Positive and negative effects of grass, cattle, and wild herbivores on *Acacia* saplings in an East African savanna. *Oecologia*, 153, 984-995.
- Ripple, W.J. & Beschta, R.L. (2007) Restoring Yellowstone's aspen with wolves. *Biological Conservation*, 138, 514-519.

- Rutina, L.P., Moe, S.R. & Swenson, J.E. (2005) Elephant *Loxodonta africana* driven woodland conversion to shrubland improves dry-season browse availability for impalas *Aepyceros melampus*. *Wildlife Biology*, 11, 207-213.
- Sankaran, M., Ratnam, J. & Hanan, N. (2008) Woody cover in African savannas: the role of resources, fire and herbivory. *Global Ecology and Biogeography*, 17, 236-245.
- Scholes, R.J. & Walker, B.H. (1993) *An African savanna: synthesis of the Nylsvlei study*. Cambridge University Press.
- Scholes, R.J. & Mennell, K.G. (2008) *Elephant management: a scientific assessment for South Africa*. Wits University Press, Johannesburg.
- Slotow, R., Garaï, M.E., Reilly, B., Page, B. & Carr, R.D. (2005) Population dynamics of elephants re-introduced to small fenced reserves in South Africa. *South African Journal of Wildlife Research*, 35, 23-32.
- Seymour, C.L. (2008) Grass, rainfall and herbivores as determinants of *Acacia erioloba* (Meyer) recruitment in an African savanna. *Plant Ecology*, 197, 131-138.
- Shannon, G., Matthews, W.S., Page, B.R., Parker, G.E. & Smith, R.J. (2009) The affects of artificial water availability on large herbivore ranging patterns in savanna habitats: a new approach based on modelling elephant path distributions. *Diversity and Distributions*, 15, 776-783.
- Shaw, M.T., Keesing, F. & Ostfeld, R.S. (2002) Herbivory on *Acacia* seedlings in an East African savanna. *Oikos*, 98, 385-392.
- Siebert, F. & Eckhardt, H.C. (2008) The vegetation and floristics of the Nkhuflu exclosures, Kruger National Park. *Koedoe*, 50, 126-144.
- Skarpe, C., Aarrestad, P.A., Andreassen, H.P., Dhillion, S.S., Dimakatso, T., Du Toit, J.T., Duncan, Halley, J., Hytteborn, H., Makhabu, S., Mari, M., Marokane, W., Masunga, G., modise, D., Moe, S.R., Mojaphoko, R., Mosugelo, D., Motsumi, S., Neo-Mahupeleng, G., Ramotadima, M., Rutina, L., Sechele, L., Sejoie, T.B., Stokke, S., swenson, J.E., Taolo, C., Vandewalle, M. & Wegge, P. (2004) The return of the giants: ecological effects of an increasing elephant population. *Ambio*, 33, 276-282.
- Staver, A.C., Bond, W.J., Stock, W.D., Jansen van Rensburg, S. & Waldram, M.S. (2009) Browsing and fire interact to suppress tree density in an African savanna. *Ecological Applications*, 19, 1909-1919.
- Tilman, D., Knops, J.M.H., Wedin, D., Reich, P., Ritchie, M. & Siemann, E. (1997) The influence of functional diversity and composition on ecosystem processes. *Science*, 277, 1300-1302.

- Valeix, M., Chamaillé-Jammes, S. & Fritz, H. (2007a) Interference competition and temporal niche shifts: elephants and herbivore communities at waterholes. *Oecologia*, 153, 739-748.
- Valeix, M., Fritz, H., Dubois, S., Kanengoni, K., Alleaume, S. & Saïd, S. (2007b) Vegetation structure and ungulate abundance over a period of increasing elephant abundance in Hwange National Park, Zimbabwe. *Journal of Tropical Ecology*, 23, 87-93.
- Valeix, M., Fritz, H., Sabatier, R., Murindagomo, F., Cumming, D. & Duncan, P. (2011) Elephant-induced structural changes in the vegetation and habitat selection by large herbivores in an African savanna. *Biological Conservation*, 144, 902-912.
- Van Aarde, R.J., Ferreira, S.M., Jackson, T.P., Page, B., de Beer, Y., Gouch, K., Guldmond, R., Junker, J., Olivier, P., Ott, T. & Trimble, M. (2008) Elephant population biology and ecology. *Elephant management: A scientific assessment for South Africa* (ed. by M.C. Scholes and K.G. Mennell), pp. 84-145. Wits University Press, Johannesburg.
- Van de Koppel, J. & Prins, H.H.T. (1998). The importance of herbivore interactions for the dynamics of African savanna woodlands; an hypothesis. *Journal of Tropical Ecology*, 14, 565-576.
- van Wilgen, B.W., Govender, N., Biggs, H.C., Ntsala, D. & Funda, X.N. (2004) Response of savanna fire regimes to changing fire-management policies in a large African National Park. *Conservation Biology*, 18, 1533-1540.
- Vanak, A.T., Shannon, G., Thaker, M., Page, B., Grant, R. & Slotow, R. (2011) Biocomplexity in large tree mortality: interaction between elephant, fire and landscape in an African savanna. *Ecography*, doi: 10.1111/j.1600-0587.2011.07213.x
- Wigley, B.J., Bond, W.J. & Hoffman, M.T. (2010) Thicket expansion in a South African savanna under divergent land use: local vs. global drivers? *Global Change Biology*, 16, 964-976.
- Young, K.D. & Van Aarde, R.J. (2011) Science and elephant management decisions in South Africa. *Biological Conservation*, 144, 876-885.

**Appendix S2.1.** List of tree species recorded in each of the seven reserves

Species	KNP	MGR	GMPGR	MkGR	PPGR	PNP	PGR
<i>Acacia ataxacantha</i> DC.	x		x	x	x		
<i>Acacia borleae</i> Burt Davy				x	x		x
<i>Acacia burkei</i> Benth.	x	x	x	x	x	x	
<i>Acacia caffra</i> (Thunb.) Willd.	x	x		x	x	x	x
<i>Acacia erioloba</i> E.Mey.		x					
<i>Acacia erubescens</i> Welw. ex Oliv.		x					
<i>Acacia exuvialis</i> I. Verd.	x		x				
<i>Acacia gerrardii</i> Benth.	x	x	x	x	x	x	
<i>Acacia grandicornuta</i> Gerstner	x	x		x	x	x	
<i>Acacia karroo</i> Hayne		x	x	x	x	x	x
<i>Acacia luederitzii</i> Engl.				x	x		x
<i>Acacia mellifera</i> (Vahl) Benth.		x				x	
<i>Acacia nigrescens</i> Oliv.	x	x	x	x		x	x
<i>Acacia nilotica</i> (L.) Wild. ex Delile	x	x	x	x	x	x	x
<i>Acacia robusta</i> Burch.	x	x	x		x	x	x
<i>Acacia schweinfurthii</i> Brenan & Exell			x	x	x		
<i>Acacia senegal</i> (L.) Willd.				x	x		x
<i>Acacia sieberiana</i> DC.				x			
<i>Acacia tortilis</i> (Forssk.) Hayne	x	x		x	x	x	x
<i>Acacia welwitschii</i> Oliv.	x						
<i>Acacia xanthophloea</i> Benth.				x	x		x
<i>Acalypha glabrata</i> Thunb.	x	x				x	
<i>Acalypha sonderiana</i> Müll. Arg.					x		
<i>Acokanthera oppositifolia</i> (Hochst.) Codd						x	
<i>Albizia adianthifolia</i> (Schumach.) W. Wight					x		
<i>Albizia anthelmintica</i> (A. Rich.) Brongn.				x			
<i>Albizia harveyi</i> Fourn.	x		x				
<i>Albizia petersiana</i> (Bolle) Oliv.	x						
<i>Allophylus africanus</i> P. Beauv.				x			
<i>Allophylus dregeanus</i> (Sond.) De Winter				x			
<i>Annona senegalensis</i> Pers.						x	
<i>Apodytes dimidiata</i> E. Mey. ex Arn.					x		
<i>Azima tetracantha</i> Lam.				x	x		x
<i>Balanites maughamii</i> Sprague	x		x	x	x		x
<i>Balanites pedicellaris</i> Mildbr. & Schltr.							x
<i>Berchemia discolor</i> (Klotzsch) Hemsl.	x						
<i>Berchemia zeyheri</i> (Sond.) Grubov		x	x	x	x	x	x
<i>Bolusanthus speciosus</i> (Bolus) Harms	x		x	x			x
<i>Boscia albitrunca</i> (Burch.) Gilg & Gilg-Ben.		x	x			x	
<i>Boscia foetida</i> Schinz	x	x				x	
<i>Boscia mossambicensis</i> Klotzsch	x						
<i>Brachylaena discolor</i> DC.				x	x	x	
<i>Bridelia mollis</i> Hutch.		x					
<i>Buddleja salviifolia</i> (L.) Lam.						x	
<i>Burkea africana</i> Hook.						x	

Species	KNP	MGR	GMPGR	MkGR	PPGR	PNP	PGR
<i>Cadaba natalensis</i> Sond.	x			x			x
<i>Cadaba termitaria</i> N.E.Br.		x					
<i>Callichilia orientalis</i> S.Moore					x		
<i>Calodendrum capense</i> (L.f.) Thunb.					x		
<i>Canthium ciliatum</i> (Klotzsch) Kuntze				x			
<i>Canthium gilfillanii</i> (N.E.Br.) O.B.Mill.		x					
<i>Canthium inerme</i> (L.f.) Kuntze							x
<i>Canthium setiflorum</i> Hiern				x	x		
<i>Canthium suberosum</i> Codd							x
<i>Capparis sepiaria</i> L.	x			x			
<i>Capparis tomentosa</i> Lam.	x			x	x		x
<i>Carissa bispinosa</i> (L.) Desf. ex Brenan	x	x		x	x	x	x
<i>Carissa edulis</i> (Forssk.) Vahl			x				
<i>Carissa macrocarpa</i> (Eckl.) A.DC.				x	x		
<i>Carissa tetramera</i> (Sacleux) Stapf				x	x		
<i>Casearia gladiiformis</i> Mast.					x		
<i>Cassia abbreviata</i> Oliv.	x						
<i>Catunaregam</i> sp. A				x			x
<i>Celtis africana</i> Burm.f.		x		x	x	x	
<i>Chaetachme aristata</i> E.Mey. Ex Planch.				x	x	x	
<i>Cleistanthus schlechteri</i> (Pax) Hutch.				x	x		
<i>Coddia rudis</i> (E.Mey. ex Har.) Verdc.				x	x		
<i>Cola greenwayi</i> Brenan					x		
<i>Colophospermum mopane</i> (kirk ex Benth.) J.Léonard	x		x				
<i>Combretum apiculatum</i> Sond.	x	x	x	x	x	x	x
<i>Combretum erythrophyllum</i> (Burch.) Sond.		x				x	x
<i>Combretum hereroense</i> Schinz	x	x	x				
<i>Combretum imberbe</i> Wawra	x	x	x	x		x	
<i>Combretum microphyllum</i> Klotzsch	x						x
<i>Combretum molle</i> R.Br. ex G.Don		x	x	x	x	x	
<i>Combretum zeyheri</i>	x	x		x		x	
<i>Commiphora africana</i> (A.Rich.) Engl.	x	x	x				x
<i>Commiphora glandulosa</i> Schinz			x				
<i>Commiphora harveyi</i> (Engl.) Engl.	x		x				
<i>Commiphora mollis</i> (Oliv.) Engl.			x				
<i>Commiphora neglecta</i> I.Verd.			x	x	x		x
<i>Commiphora pyracanthoides</i> Engl.	x		x	x			x
<i>Commiphora schimperi</i> (O.Berg) Engl.	x	x				x	
<i>Commiphora zanzibarica</i> (Baill.) Engl.	x						
<i>Cordia caffra</i> Sond.				x			
<i>Cordia ovalis</i> R.Br ex A.DC	x						x
<i>Croton gratissimus</i> Burch.						x	
<i>Croton megalobotrys</i> Müll.Arg.	x		x				
<i>Croton menyharthii</i> Pax				x			
<i>Croton pseudopulchellus</i> Pax					x		
<i>Croton steenkampianus</i> Gerstner					x		

Species	KNP	MGR	GMPGR	MkGR	PPGR	PNP	PGR
<i>Croton sylvaticus</i> Hochst. ex C.Krauss				x			
<i>Cryptocarya woodii</i> Engl.					x		
<i>Cussonia spicata</i> Thunb.					x	x	
<i>Dalbergia melanoxylo</i> n Guill. & Perr.	x		x				
<i>Dalbergia nitidula</i> Welw. ex Baker					x		
<i>Dalbergia obovata</i> E.Mey.					x		
<i>Deinbollia oblongifolia</i> (E.Mey. ex Arn.) Radlk.					x		
<i>Dialium schlechteri</i> Harms					x		
<i>Dichrostachys cinerea</i> (L.) Wight & Arn.	x	x	x	x	x	x	x
<i>Diospyros inhacaensis</i> F.White					x		
<i>Diospyros lycioides</i> Desf.		x		x	x	x	
<i>Diospyros mespiliformis</i> Hochst. ex A.DC.	x		x				
<i>Diospyros natalensis</i> (Harv.) Brenan				x			
<i>Diospyros simii</i> (Kuntze) De Winter							x
<i>Diospyros villosa</i> (L.) De Winter						x	
<i>Diospyros whyteana</i> (Hiern) F.White		x				x	
<i>Dodonaea viscosa</i> Jacq.				x			
<i>Dombeya burgessiae</i> Gerrard ex Harv.							x
<i>Dombeya cymosa</i> Harv.				x			
<i>Dombeya rotundifolia</i> (Hochst.) Planch.		x	x	x	x	x	
<i>Dovyalis caffra</i> (Hook.f. & Harev.) Hook.f.				x	x	x	x
<i>Dovyalis longispina</i> (Harv.) Warb.				x	x	x	x
<i>Dovyalis zeyheri</i> (Sond.) Warb.						x	
<i>Drypetes arguta</i> (Müll.Arg.) Hutch.					x		
<i>Drypetes gerrardii</i> Hutch.					x		
<i>Ehretia amoena</i> Klotzsch	x		x				x
<i>Ehretia rigida</i> (Thunb.) Druce		x	x	x	x	x	x
<i>Ekebergia capensis</i> Sparrm.					x		
<i>Elaeodendron croceum</i> (Thunb.) DC.				x			
<i>Elaeodendron transvaalense</i> (Burt Davy) R.H.Archer	x		x	x	x		x
<i>Englerophytum magalismontanum</i> (Sond.) T.D.Penn.		x					
<i>Erythrina humeana</i> Spreng.				x			
<i>Erythrina lysistemon</i> Hutch.						x	
<i>Erythrocca berberidea</i> Prain				x			
<i>Erythroxyllum delagoense</i> Schinz.				x	x		
<i>Erythroxyllum emarginatum</i> Thonn.					x		
<i>Euclea crispa</i> (Thunb.) Gürke		x		x	x	x	
<i>Euclea divinatorum</i> Hiern	x		x	x	x	x	x
<i>Euclea natalensis</i> A.DC.	x	x	x	x	x	x	x
<i>Euclea racemosa</i> Murray				x	x	x	x
<i>Euclea undulata</i> Thunb.		x	x	x	x	x	x
<i>Eugenia capensis</i> (Eckl. & Zeyh.) Harv. ex Sond.					x		
<i>Faurea saligna</i> Harv.						x	

Species	KNP	MGR	GMPGR	MkGR	PPGR	PNP	PGR
<i>Ficus burkei</i> (Miq.) Miq.						X	
<i>Ficus capreifolia</i> Delile				X			
<i>Ficus ingens</i> (Miq.) Miq.						X	
<i>Ficus natalensis</i> Hochst.			X				
<i>Ficus sycomorus</i> L.			X	X			
<i>Flueggea virosa</i> (Roxb. ex Willd.) Voigt	X	X	X	X		X	
<i>Galpinia transvaalica</i> N.E.Br.				X	X		
<i>Gardenia cornuta</i> Hemsl.				X	X		
<i>Gardenia volkensii</i> K.Schum	X	X	X	X	X		X
<i>Grewia bicolor</i> Juss.	X	X	X	X	X	X	X
<i>Grewia caffra</i> Meisn.				X	X	X	X
<i>Grewia flava</i> DC.		X	X	X	X	X	X
<i>Grewia flavescence</i> Juss.	X	X	X	X		X	X
<i>Grewia hexamita</i> Burret	X			X			X
<i>Grewia microthyrsa</i> K.Schum. ex Burret			X	X	X		X
<i>Grewia monticola</i> Sond.	X	X	X	X	X	X	X
<i>Grewia occidentalis</i> L.		X		X	X	X	X
<i>Grewia retinervis</i> Burret		X					
<i>Grewia villosa</i> Willd.	X		X			X	X
<i>Gymnosporia arenicola</i> M.Jordaan				X			
<i>Gymnosporia buxifolia</i> (L.) Szyszyl.		X	X	X	X	X	X
<i>Gymnosporia maranguensis</i> (Loes.) Loes.	X						
<i>Gymnosporia nemorosa</i> (Eckl. & Zeyh.) Szyszyl.				X			X
<i>Gymnosporia polyacantha</i> (Sond.) Szyszyl.						X	
<i>Gymnosporia senegalensis</i> (Lam.) Loes.	X	X	X	X	X	X	X
<i>Harpephyllum caffrum</i> Bernh. ex C.Krauss				X			
<i>Hippobromus pauciflorus</i> (L.f.) Radlk.						X	
<i>Hymenocardia ulmoides</i> Oliv.					X		
<i>Hyperacanthus amoenus</i> (Sims) Bridson				X	X		
<i>Hypericum revolutum</i> Vahl					X		
<i>Keetia gueinzii</i> (Sond.) Bridson						X	
<i>Kraussia floribunda</i> Harv.				X	X		
<i>Lagynias monteiroi</i> (Oliv.) Bridson				X			
<i>Landolphia kirkii</i> Dyer ex Hook.f.				X	X		
<i>Lannea discolor</i> (Sond.) Engl.		X	X			X	
<i>Lannea edulis</i> (Sond.) Engl.	X						
<i>Lannea schweinfurthii</i> (Engl.) Engl.	X		X			X	
<i>Lumnitzera racemosa</i> Willd.					X		
<i>Maerua angolensis</i> DC.				X			X
<i>Maerua parvifolia</i> Pax	X						
<i>Mimusops zeyheri</i> Sond.	X						
<i>Monanthotaxis caffra</i> (Sond.) Verdc.				X	X		
<i>Mundulea sericea</i> (Willd.) A.Chev.	X	X		X	X	X	
<i>Morella pilulifera</i> (Rendle) Killick						X	
<i>Morella serrata</i> (Lam.) Killick							X
<i>Mystroxydon aethiopicum</i> (Thunb.) Loes	X			X	X		X

Species	KNP	MGR	GMPGR	MkGR	PPGR	PNP	PGR
<i>Nuxia oppositifolia</i> (hochst.) Benth.			x				
<i>Obetia tenax</i> (N.E.Br.) Friis		x				x	
<i>Ochna arborea</i> Burch. ex DC.				x	x		
<i>Ochna inermis</i> (Forssk.) Penzig					x		
<i>Ochna natalitia</i> (Meisn.) Walp.					x		
<i>Olea europaea</i> L.		x	x	x		x	x
<i>Ormocarpum trichocarpum</i> (Taub.) Engl.	x		x	x	x		x
<i>Ozoroa engleri</i> R. & A.Fern.	x			x			x
<i>Ozoroa obovata</i> (Oliv.) R. & A.Fern.				x			
<i>Ozoroa paniculosa</i> (Sond.) R. & A.Fern.		x	x	x	x	x	
<i>Ozoroa sphaerocarpa</i> R. & A.Fern.	x		x			x	
<i>Pappea capensis</i> Eckl. & Zeyh.	x	x	x	x	x	x	x
<i>Pavetta edentula</i> Sond.					x		
<i>Peltophorum africanum</i> Sond.	x	x	x	x	x	x	x
<i>Philenoptera violacea</i> (Klotze) Schrire	x		x				
<i>Phyllanthus reticulatus</i> Poir.	x		x		x		
<i>Pisonia aculeata</i> L.				x			
<i>Plectroniella armata</i> (K.Schum.) Robyns	x						
<i>Pleurostyliia capensis</i> (Turcz.) Loes.					x		
<i>Psyrdrax livida</i> (Hiern) Bridson						x	
<i>Psyrdrax locuples</i> (K.Schum.) Bridson				x	x		
<i>Psyrdrax obovata</i> (Klotzsch ex Eckl. & Zeyh.) Bridson				x	x		
<i>Ptaeroxylon obliquum</i> (Thunb.) Radlk.				x			
<i>Pteleopsis myrtifolia</i> (M.A.Lawson) Engl. & Diels				x	x		
<i>Pterocarpus rotundifolius</i> (Sond.) Druce	x		x				
<i>Putterlickia verrucosa</i> (E.Mey. ex Sond.) Szyszyl.				x	x		
<i>Pyrostria hystrix</i> (Bremek.) Bridson	x		x	x	x	x	x
<i>Rawsonia lucida</i> Harv. & Sond.					x		
<i>Rhigozum brevispinosum</i> Kuntze		x				x	
<i>Rhus chiridensis</i> Baker f.					x		
<i>Rhus dentata</i> Thunb.						x	x
<i>Rhus gueinzii</i> Sond.	x			x	x	x	x
<i>Rhus lancea</i> L.f.		x				x	
<i>Rhus leptodictyai</i> Diels		x				x	
<i>Rhus lucida</i> L.						x	
<i>Rhus natalensis</i> Bernh. ex C.Krauss					x		
<i>Rhus pentheri</i> Zahlbr.					x		
<i>Rhus pyroides</i> Burch.		x		x		x	
<i>Rhus rehmanniana</i> Engl.				x			
<i>Rhus tomentosa</i> L.				x			
<i>Salacia leptoclada</i> Tul.					x		
<i>Salix mucronata</i> (Thunb.)						x	
<i>Salvadora australis</i> Schweick.				x			x
<i>Sapium ellipticum</i> (Hochst. ex C.Krauss) Pax				x	x		

Species	KNP	MGR	GMPGR	MkGR	PPGR	PNP	PGR
<i>Schotia brachypetala</i> Sond.	x		x	x	x		x
<i>Schotia capitata</i> Bolle				x			x
<i>Sclerocarya birrea</i> (A.Rich.) Hochst.	x	x	x	x	x	x	x
<i>Scolopia mundii</i> (Eckl. & Zeyh.) Warb.				x		x	
<i>Scolopia zeyheri</i> (Nees) Harv.		x		x	x	x	
<i>Scutia myrtina</i> (Burm.f.) Kurz				x	x		
<i>Senna petersiana</i> (Bolle) Lock	x				x		
<i>Sesbania sesban</i> (L.) Merr.					x		
<i>Sideroxylon inerme</i> L.				x	x	x	x
<i>Solanum aculeastrum</i> Dunal			x				
<i>Spirostachys africana</i> Sond.	x	x	x	x	x	x	x
<i>Sterculia rogersii</i> N.E.Br.	x		x				
<i>Strychnos decussata</i> (Pappe) Gilg				x	x		
<i>Strychnos henningsii</i> Gilg				x	x		
<i>Strychnos madagascariensis</i> Poir.	x		x	x	x		
<i>Strychnos mitis</i> S.Moore				x			
<i>Strychnos spinosa</i> Lam.	x			x	x	x	
<i>Suregada africana</i> (Sond.) Kuntze					x		
<i>Suregada zanzibariensis</i> Baill.					x		
<i>Syzygium cordatum</i> Hochst. ex C.Krause						x	
<i>Tabernaemontana elegans</i> Stapf					x		
<i>Tapura fischeri</i> Engl.						x	
<i>Tarchonanthus camphoratus</i> L.		x		x	x	x	
<i>Tarennia junodii</i> (Schinz) Bremek.					x		
<i>Terminalia prunioides</i> M.A.Lawson	x	x	x			x	
<i>Terminalia sericea</i> Burch. ex DC.	x	x	x	x	x	x	
<i>Toddaliopsis bremekampii</i> I.Verd.					x		
<i>Trema orientalis</i> (L.) Blume				x			
<i>Tricalysia capensis</i> (Meisn. ex Hochst.) Sim					x		
<i>Tricalysia lanceolata</i> (Sond.) Burt Davy				x	x		
<i>Tricalysia sonderiana</i> Hiern				x	x		
<i>Trichilia emetica</i> Vahl				x	x		
<i>Uvaria caffra</i> E.Mey. ex Sond.				x	x		
<i>Uvaria lucida</i> Benth.					x		x
<i>Vangueria infausta</i> Burch.					x	x	
<i>Vepris carringtoniana</i> Medonça				x			
<i>Vitex ferruginea</i> Schumach. & Thonn.					x		
<i>Vitex zeyheri</i> Sond. ex Schauer		x					
<i>Wrightia natalensis</i> Stapf					x		
<i>Ximenia americana</i> L.	x	x	x	x	x	x	x
<i>Ximenia caffra</i> Sond.		x	x	x	x	x	x
<i>Xylothea kraussiana</i> Hochst.					x		x
<i>Zanthoxylum capense</i> (Thunb.) Harv.	x			x	x	x	
<i>Ziziphus mucronata</i> Willd.	x	x	x	x	x	x	x
Number of unknown species	4	3	13	3	5	13	8

KNP: Kruger National Park; MGR: Madikwe Game Reserve; GMPGR: Greater Makalali Private Game Reserve; MkGR: Mkuze Game Reserve; PPGR: Phinda Private Game Reserve; PNP: Pilanesberg National Park; PGR: Pongola Game Reserve

**Appendix S2.2.** Backward regression models per species across all seven reserves\*

Species	Tree size	Factor	R <sup>2</sup>	d.f.	F	P	β	t	P
<i>Acacia nilotica</i>	Seedling		0.506	1,5	7.147	0.044			
		Rainfall					0.767	2.737	0.044
<i>Combretum apiculatum</i>	Seedling		0.936	2,4	45.131	0.002			
		Fire return period					0.877	8.104	0.001
		Elephant density					-0.243	-2.249	0.088
	Sapling		0.961	1,5	149.661	<0.001			
		Fire return period					0.984	12.234	<0.001
	Small tree		0.969	2,4	94.567	<0.001			
		Fire return period					1.007	13.718	<0.001
		Elephant density					0.130	1.772	0.151
	Medium tree		0.976	3,3	82.615	0.002			
		Fire return period					1.059	13.803	0.001
		Rainfall					0.098	1.304	0.283
		Elephant density					0.109	1.652	0.197
	Large tree		0.984	3,3	121.552	0.001			
		Fire return period					0.968	15.281	0.001
		Rainfall					-0.073	11.176	0.325
		Time since introduction					0.080	1.464	0.239
<i>Dichrostachys cinerea</i>	Seedling		0.764	2,4	10.734	0.025			
		Rainfall					0.864	4.225	0.013
		Elephant density					0.589	2.880	0.045
	Small tree		0.714	2,4	8.478	0.036			
		Elephant density					0.983	3.744	0.020
		Time since introduction					-0.919	-3.503	0.025

<i>Species</i>	Tree size	Factor	R <sup>2</sup>	d.f.	F	P	$\beta$	t	P
<i>Euclea natalensis</i>	Seedling		0.547	1,5	8.240	0.035			
		Rainfall					0.789	2.871	0.035
	Sapling		0.843	1,5	33.305	0.002			
		Rainfall					0.932	5.771	0.002
<i>Grewia bicolor</i>	Large tree		0.767	2,4	10.894	0.024			
		Fire return period					0.325	1.420	0.229
	Seedling	Rainfall					1.042	4.549	0.010
		Fire return period					1.278	18.243	0.003
	Sapling	Rainfall					0.552	8.020	0.015
		Elephant density					0.238	3.338	0.079
		Time since introduction					0.179	2.883	0.102
		Fire return period					1.012	20.595	<0.001
	Small tree	Time since introduction					0.286	5.830	0.004
				0.979	3,3	96.273	0.002		
Fire return period						0.935	15.206	0.001	
Elephant density						-0.251	-3.469	0.040	
Medium tree	Time since introduction					0.442	6.286	0.008	
			0.491	1,5	6.796	0.048			
<i>Grewia monticola</i>	Small tree	Time since introduction					0.759	2.607	0.048
		Fire return period					0.757	2.587	0.049
<i>Gymnosporia senegalensis</i>	Seedling		0.899	3,3	18.766	0.019			
		Fire return period					0.680	3.859	0.031
		Rainfall					1.218	7.033	0.006
<i>Peltophorum africanum</i>	Small tree	Elephant density					0.831	5.313	0.013
		Elephant density					-0.442	-3.844	0.018
		Time since introduction					1.155	10.029	0.001

Species	Tree size	Factor	R <sup>2</sup>	d.f.	F	P	β	t	P
<i>Sclerocarya birrea</i>	Seedling		0.817	2,4	14.384	0.015			
		Fire return period					0.982	5.351	0.006
	Sapling	Elephant density	0.363	1.979	0.119				
			0.894	3,3	17.927	0.020			
		Fire return period					-0.168	-1.044	0.373
	Rainfall	-0.309					-1.948	0.147	
	Small tree	Time since introduction	0.875	6.283	0.008				
			0.874	3,3	0.446	0.026			
		Fire return period					-0.318	-1.619	0.204
	Rainfall	-0.392					-2.031	0.135	
	Large tree	Elephant density	-1.114	-6.386	0.008				
			0.969	2,4	94.256	<0.001			
Fire return period		0.889					10.609	<0.001	
Rainfall	-0.174	-2.080					0.106		
<i>Spirostachys africana</i>	Sapling		0.864	3,3	13.672	0.030			
		Fire return period					-0.333	-1.626	0.202
		Rainfall					0.440	2.188	0.116
	Small tree	Elephant density	-0.685	-3.774	0.033				
			0.869	2,4	20.894	0.008			
		Rainfall					0.731	4.716	0.009
	Elephant density	-0.461					-3.026	0.039	
	Medium tree		0.766	2,4	10.806	0.024			
		Rainfall					0.753	3.696	0.021
	Large tree	Elephant density	-0.372	-1.826	0.142				
			0.801	2,4	13.087	0.018			
		Rainfall					0.876	4.789	0.009
Time since introduction	-0.243	-1.331					0.254		

\* No significant models were found for *Pappea capensis* and *Ziziphus mucronata*

**Appendix S3.1.** List of 19 species included in the population structure, functional height class and browsing pressure analyses.

<i>Acacia erubescens</i> Welw. ex Oliv.	<i>Lannea schweinfurthii</i> (Engl.) Engl.
<i>Acacia nigrescens</i> Oliv.	<i>Ozoroa</i> spp.
<i>Boscia albitrunca</i> (Burch.) Gilg & Gilg-Ben.	<i>Peltophorum africanum</i> Sond.
<i>Cassia abbreviata</i> Oliv.	<i>Sclerocarya birrea</i> (A.Rich.) Hochst.
<i>Combretum apiculatum</i> Sond.	<i>Sterculia rogersii</i> N.E.Br.
<i>Combretum mossambicense</i> (Klotzsch) Engl.	<i>Terminalia prunioides</i> M.A. Lawson
<i>Commiphora africana</i> (A.Rich.) Engl.	<i>Jasminum multipartitum</i> Hochst.
<i>Commiphora mollis</i> (Oliv.) Engl.	<i>Ximenia americana</i> L.
<i>Dichrostachys cinerea</i> (L.) Wight & Arn.	<i>Ziziphus mucronata</i> Willd.
<i>Grewia</i> spp.	

**Appendix S4.1.** Regression analyses for tree abundance vs. tree diameter.

Species	Treatment	Slope	Intercept	R <sup>2</sup>	Significance
<i>Salacia leptoclada</i>	Open access (+E+N) <sup>a</sup>	-3.024	8.730	0.917	**
	Partial enclosure (-E+N) <sup>b</sup>	-2.776	8.204	0.842	**
	Full enclosure (-E-N) <sup>c</sup>	-2.942	8.712	0.953	**
<i>Uvaria caffra</i>	Open access (+E+N) <sup>a</sup>	-2.539	7.464	*.792	**
	Partial enclosure (-E+N) <sup>b</sup>	-2.936	7.792	0.925	**
	Full enclosure (-E-N) <sup>c</sup>	-2.677	7.926	0.922	**
<i>Tricolysia junodii</i>	Open access (+E+N) <sup>a</sup>	-4.152	8.466	0.741	*
	Partial enclosure (-E+N) <sup>b</sup>	-3.847	7.883	0.613	*
	Full enclosure (-E-N) <sup>c</sup>	-4.642	9.196	0.839	**
<i>Dialium schlechteri</i>	Open access (+E+N) <sup>a</sup>	-0.465	1.382	0.367	*
	Partial enclosure (-E+N) <sup>b</sup>	-0.541	1.908	0.296	**
	Full enclosure (-E-N) <sup>c</sup>	-0.352	1.505	0.151	-
<i>Newtonia hildebrandtii</i>	Open access (+E+N) <sup>a</sup>	-0.390	1.487	0.142	-
	Partial enclosure (-E+N) <sup>b</sup>	-0.354	1.442	0.135	-
	Full enclosure (-E-N) <sup>c</sup>	-0.338	1.397	0.087	-
<i>Pteleopsis myrtifolia</i>	Open access (+E+N) <sup>a</sup>	-0.689	2.387	0.357	*
	Partial enclosure (-E+N) <sup>b</sup>	-0.519	1.981	0.352	*
	Full enclosure (- E-N) <sup>c</sup>	-0.926	3.287	0.419	**

Regressions were performed for each of six tree species for each of the three enclosure treatments in the Sand Forest of Phinda Private Game Reserve, South Africa. A steep negative slope indicates an increasing population (i.e. a high abundance of seedlings and a low abundance of tall trees), whereas a negative slope close to zero indicates a disrupted distribution with many large trees and little regeneration.

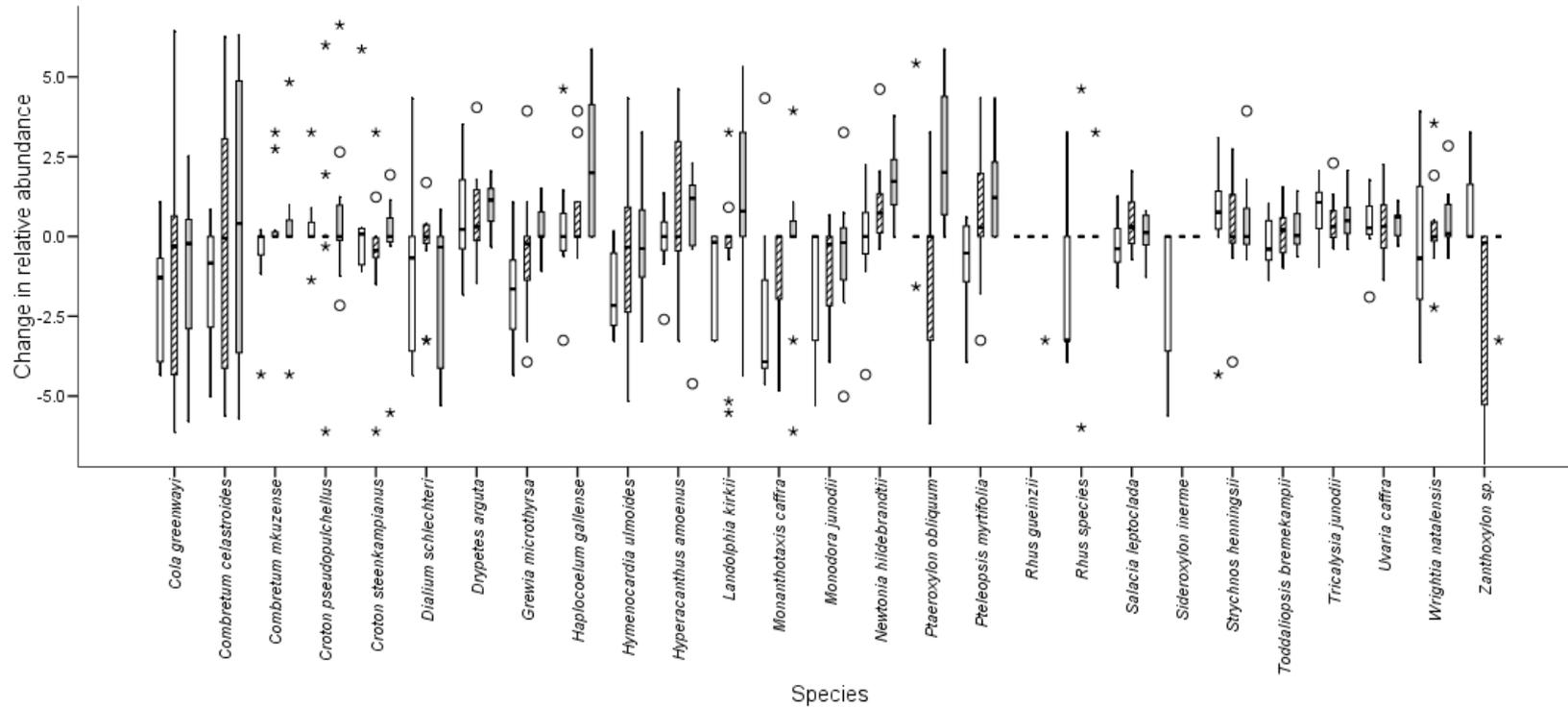
\* P < 0.05; \*\* P < 0.01; -, non significant (P > 0.05)

<sup>a</sup> Unfenced area accessible for all herbivores; <sup>b</sup> Area fenced to exclude elephant; <sup>c</sup> Area fenced to exclude nyala and elephant, but accessible to smaller herbivores

**Appendix S5.1.** List of 27 species included in the analyses

<i>Cola greenwayi</i> Brenan	<i>Newtonia hildebrandtii</i> (Vatke) Torre
<i>Combretum celastroides</i> Welw. Ex Laws.	<i>Ptaeroxylon obliquum</i> (Thunb.) Radlk.
<i>Combretum mkuzense</i> Carr & Retief	<i>Pteleopsis myrtifolia</i> (Laws.) Engl. & Diels
<i>Croton pseudopulchellus</i> Pax	<i>Rhus gueinzii</i> Sond.
<i>Croton steenkampianus</i> Gerstner	<i>Rhus natalensis</i> Bernh. Ex Krauss
<i>Dialium schlechteri</i> Harms	<i>Salacia leptoclada</i> Tul.
<i>Drypetes arguta</i> (Muell. Arg.) Hutch	<i>Sideroxylon inerme</i> L.
<i>Grewia microthyrsa</i> K. Schum. Ex Burret	<i>Strychnos henningsii</i> Gilg
<i>Haplocoelum gallense</i> (Engl.) Radlk.	<i>Toddalopsis bremekampii</i> Verdoorn
<i>Hymenocardia ulmoides</i> Oliv.	<i>Tricalysia junodii</i> (Schinz) Brenan
<i>Hyperacanthus amoenus</i> (Sims) Bridson	<i>Uvaria caffra</i> E. Mey. Ex Sond.
<i>Landolphia kirkii</i> T.-Dyer	<i>Wrightia natalensis</i> Stapf
<i>Monanthotaxis caffra</i> (Sond.) Verdc.	<i>Zanthoxylum</i> sp.
<i>Monodora junodii</i> Engl. & Diels	

**Appendix S5.2.** The short-term effects in the relative changes in tree species abundances between 2005 and 2007 per tree species per treatment: full access (competition and facilitation both elephant and nyala: open bars), partial exclusion (competitive release nyala: diagonal hatching) and full exclusion (competitive release both elephant and nyala: gray bars). Data are for range (whiskers), 25% and 75% quartiles (box), and median (line). N= 7 replicates for the full access treatment and N= 12 for both the partial and full exclusion.



**Appendix S5.3.** The ANOVA tables of the analyses

Dependent variables	Factors	d.f.	F	P
Turnover between 2005-2007	Treatment	2,28	3.416	0.047
Diet diversity (log <sub>10</sub> -transformed)	Treatment	2,65	2.811	0.034 (1-tailed)
	Herbivore group	2,65	1.386	0.129 (1-tailed)
	Treatment x Herbivore group	1,65	0.015	0.452 (1-tailed)
Diet breadth	Herbivore group	2,68	0.445	0.322 (1-tailed)
Resource specificity				
Nyala open access vs. partial enclosure	Treatment	1,22	5.338	0.031
Small-size herbivores open access vs. partial enclosure	Treatment	1,22	6.699	0.017
Within open access treatment	Herbivore group	1,32	3.164	0.056
Within partial enclosure	Herbivore group	1,22	5.234	0.032
Diet overlap nyala small-size herbivores in partial enclosure (square root transformed)	Herbivore group	1,22	0.146	0.706
Browsing pressure				
Nyala	Treatment	1,22	3.621	0.035 (1-tailed)
Small-size herbivores	Treatment	2,22	4.716	0.010 (1-tailed)
	Site	11,22	2.819	0.019

